MAIZE GROWTH AND TEMPERATURE IN THE KENYA HIGHLANDS

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Thesis submitted to the University of Nottingham
for the degree of Doctor of Philosophy

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May, 1979

ACKNOWLEDGEMENTS

I am very grateful to the following for their help during this work : Professor J.L. Monteith for guidance; Dr. P.J.N. Cooper for advice and discussion; Philip, Nyongesa, Gitau and other staff of N.A.R.S., Kitale for their hard work; Dr. B. Marshall for his advice on photosynthesis measurements; Mrs P. Arnold, Mrs J. Young and Miss L. Downes for their careful typing.

The work was supported by the Ministry of Overseas Development, London, and the Ministry of Agriculture, Nairobi.

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ABSTRACT

Field experiments were conducted at Kitale, Kenya to investigate the effects of early soil warming on growth and yield of Zea mays. In the first of these experiments (1976) a polythene mulch was applied to warm the soil of late planted maize. In the second experiment (1977) maize with a mulch was planted at three intervals after the start of the rainy season.

These two experiments showed that warming soils by 5 - 6°C caused a small increase (1 - 2) in number of leaves initiated, but early leaves were smaller and thus total leaf area produced was unaffected. Spikelet initiation began 2 - 3 weeks after the apical meristem emerged above ground level, and as the embryonic cobs were in the aerial environment; soil warming did not affect the number of spikelets initiated. The grain number at harvest, which was the major variable of the yield components, was found to be determined by the survival rate of initiated spikelets. A subsidiary trial, involving the use of different plant populations, showed similar numbers of spikelets initiated by plants of different size and growth rate.

The field experiments also showed that plant size at any stage is not a discriminant of yield, but a good relationship was found between growth rate during the 'linear' phase of growth and final grain number. A decrease of 30% in crop growth in late planted maize (1977) was associated with a decrease in mean early soil temperature of 0.7°C.

Controlled environment studies at Sutton Bonington, England, showed that an increase of early soil temperature (ca 6°C at the meristem

depth) increased the photosynthesis rate of subsequent leaves by about 20% but this increase is not consistent with changes in growth rate observed in field experiments at Kitale. These findings do not support the hypothesis that poor yields of late planted maize are a result of decreases in soil temperature. Previously discarded hypotheses based on the leaching of nutrients should be re-examined.

1. INTRODUCTION

In tropical areas with one rainfall season it has long been observed that the yields of annual crops tend to decline when planting is delayed after the rains start (Hemingway, 1955; Moberly, 1962; Goldson, 1963). For example, records from Tanzania collected by Akehurst and Screedharan (1965) show substantial reductions in the yields of maize, groundnuts, soybeans, wheat, pyrethrum, simsim, cotton and sorghum. One of the earliest explanations for this 'time of planting' effect came from Birch (1960) whose laboratory studies showed that dried soils released large amounts of mineral nutrients on rewetting. Birch suggested that these nutrients, primarily nitrogen, were likely to be leached by heavy rain and consequently were less available to later planted crops. However, other workers realised that if this were so, the time of planting effect should be supressed by the application of fertilizers. In fact, later planted crops responded less to fertilizer than earlier plantings (Akehurst and Screedharan, 1965; Semb and Garberg, 1969; Allen, 1972). Other studies showed that the 'Birch effect' is less evident in the field that in the laboratory (Cooper, 1971). Turner (1965) showed that later planted crops in Tanzania were likely to run into water deficits during the later stages of crop growth, and found a high correlation between maize yield and rainfall in the 20 day period immediately after tasselling ($r = 0.74$). However, he added that the time of planting effect was also evident in wet years, and even occurred with irrigated crops and rice grown in paddy fields - a response he could not explain.

Extensive trials by Allan (1972) showed that contemporary theories could not explain the pronounced time of planting effect on maize in the Highlands of Western Kenya. He concluded that poor soil physical conditions were responsible. In an artificial watering experiment he found that increasing amounts of water applied during the period from planting to five weeks after emergence reduced early growth, number of kernels produced and grain yield. Together with these results and a study of rainfall distribution patterns he suggested that poor soil aeration was the principal factor causing yield reductions in late planted maize. However, measurements of soil aeration by Cooper (1975) did not support this hypothesis and showed that soil aeration never became critical, even for late planted maize in very wet years.

Subsequent work at Kitale by Cooper and Law (1977) showed that there was a strong relationship between the size of plant at five weeks after emergence and the final grain yield. They found that differences in the rate of dry matter production during early growth could be explained entirely by differences in soil temperature, coupled with a moisture stress factor. Furthermore, they found a strong correlation between grain yield and soil temperature during the five weeks after emergence. As the rainy season progresses, the mean soil temperature decreases due to the increased cloud cover and evaporative cooling: values ca. 26°C in February and March decline to ca. 18°C at the peak of the rains in July/August (Law and Cooper, 1976).

Further evidence of the importance of soil temperature was obtained through the use of mulches. Polythene and hay mulches,

which respectively raised and lowered the soil temperature were associated with correspondingly higher and lower yields. The maximum effect of the mulch was achieved with as little as three weeks coverage, and longer periods were no more effective. Further mulching trials, using polythene placed over late planted maize at planting, and removed at one week increments until five weeks after emergence, confirmed this and showed increasing yields with up to three weeks soil warming, and thereafter no further advantage (Cooper and Law, 1978a). This yield increase was due mainly to the increased number of cobs and grains per plant. Using polythene mulches in this way, increased the yields of late planted maize to that of early planted maize, the only treatment at Kitale which has been able to do this.

How then does soil temperature during these early stages affect the growth of the crop? Time of planting trials showed a strong correlation between the total shoot dry weight at tasselling (W) and the final grain yield per plant (Y), according to the equation:

$Y = 0.90W - 40.5$ $\quad r = 0.96, \; p < 0.01$ (Cooper and Law 1978a)

Similar effects were found in time of planting trials in Tanzania (Turner, 1965). According to Cooper and Law (1978a) this relationship between plant size and final yield (per plant) can be traced back to the weight of plant at five weeks after emergence (W_5):

$Y = 10.1W_5 + 11.9$ $\quad r = 0.94, \; p < 0.01$

The early period of crop growth thus appeared critical in

determining the potential grain yield of the crop. Adverse conditions later, such as drought or hail, could reduce this potential, but nothing could compensate later for poor early growth. Because of the observed differences in plant size at tasselling resulting from time of planting experiments, the hypothesis was put forward that large plants are more fully able to realise the genetic yield potential. Mulching experiments, however, do not show such a difference in plant size at this stage (although they do at the five week stage) and thus it was concluded that plant size *per se* at tasselling was not critical.

During the early stages of the life of a maize plant, the apical meristem is below soil level, and hence developmental rate is largely dependent on soil temperature (see section 2.1). About five weeks after emergence (under normal Kitale conditions, three weeks after emergence under a polythene mulch) the apical meristem rises above ground level and shoot development rate becomes more dependent on air temperature. As a young maize shoot is composed almost solely of leaves, and leaf expansion is controlled by soil temperature, it appears that the increased size of the plant during the early stages at Kitale was due to a greater developmental rate, rather than increases in leaf size.

As the yield increases associated with warmer soils were due to a larger grain number, it was suggested by Law and Cooper (1976) that early vigorous growth in some way affected the initiation and number of florets produced.

Work described in this thesis was designed to investigate relationships between soil temperature and early plant development, and to explore the consequence of these relations for grain

development and final yield. More specifically, the objectives were to assess the relation with soil temperature, and the importance for yield determination of the following physiological processes:

a) Production and final number of spikelets.

b) Production and final size of leaf area.

c) Crop growth rate.

d) Leaf/crop photosynthetic efficiency.

2. ECOLOGICAL ASPECTS OF MAIZE GROWTH

2.1 Soil temperature and maize growth

It is pertinent to review effects of root temperature on plant growth, and some of the specific responses of maize. Nielsen (1974) reviewed work on root temperature, stating that all the known functions of roots are dependent on temperature. Briefly these functions and related temperature effects are as follows:

a) Water uptake. The viscosity of water increases with decreasing temperature, and cellular membranes usually become less permeable to water and solutes as temperature decreases. Many workers have reported decreased water uptake with decreased root zone temperature (e.g. Rahman and Bierhuizen, 1959; Cox and Boersma , 1967; Kleinendorst and Brouwer, 1970). Kramer (1956) suggested that the additive effects of temperature on water viscosity and protoplasm permeability decrease water uptake at 5°C to one-fourth of the rate at 25°C. Any decrease in water uptake is obviously important when considering possible water stress conditions, especially in tropical plants where transitory water stress may be present at midday even when the soil is at field capacity.

b) Nutrient uptake. Soil temperature will influence the rate of release of nutrients from organic and inorganic forms, the uptake of nutrients by plant roots and the assimilation of absorbed nutrients into complex organic compounds and subsequent translocation to above ground portions of the plant.

c) Translocation and sink relationships. Low temperatures may inhibit translocation of photosynthetic products to the root from the shoot, and it has been suggested that the resulting accumulation in the leaves depresses photosynthesis and yield (Davis and Lingle, 1961; Hartt, 1965).

d) Assimilation. Nitrogen, absorbed into the roots in ionic form, is usually converted to organic form for transport to the shoot. Accumulation of NO_3^- in the roots has been reported at extreme temperatures (Watschke et al, 1970).

e) Growth metabolites. Cytokinins and other growth regulators are produced in the root. Guinn and Hunter (1968) suggested that since low temperatures slow down all metabolic activities in roots, the production of growth regulating compounds would also be regulated. Atkin et al, (1973) have measured temperature induced changes in the export of growth regulators from the roots of maize.

In addition to changes in function, differences of temperature can be related to changes in the morphology and distribution of roots. At cooler temperatures, roots are usually whiter, thicker and less branched (Ketellapper, 1960). At high temperatures roots become filamentous.

This brief summary makes the point that soil temperature can affect the plant in many ways. Compared with other plant parts, however, the study of roots has been neglected, due to the obvious difficulties of measurement. Consequently little information is available to form a comprehensive picture of the interaction between root temperature and plant growth, and in particular,

to single out those processes which might be relevant to this study. The next step is to consider agronomic experiments in which soil temperature changes have led to a change in subsequent development and yield.

Hedrick (1905) recognised that 'in our efforts to till the soil and grow plants, we increase rather than diminish the importance of soil heat as a factor in plant life'. He urged that studies be undertaken to provide accurate knowledge of the reaction of soil temperature to the growth of cultivated plants. Earlier still, Haberlandt (as quoted by Willis et al, 1957) noted in 1874 that the maximum, optimum and minimum temperatures for maize emergence were approx. 9.5°C, 34°C and 46°C respectively. Lehenbauer (1914) varied the temperature at which maize was grown in the greenhouse, although he did not alter soil and air temperatures independently. He found that a variation in root and shoot temperature had a marked effect on the rate of elongation of the shoot. Also about this time Bouyoucos (1913) measured soil temperature differences at 3 and 5 inches under white sand compared with the same sand dyed black. However it was not until later that the interaction between soil mulching and plant growth was more fully investigated.

The use of polythene mulches to raise the yield of horticultural crops became common in America in the 1950's. Clarkson (1960) attributed these higher yields to the higher temperatures associated with the mulch, and improved nitrogen retention. Van Wijk et al (1959) and Burrows et al (1962) showed that a crop residue mulch reduced soil temperature and

decreased the early growth of corn. Allmaras et al reported that dry matter during the early stages was linearly related to the soil temperature 4 inches deep. When Knoll et al (1964) investigated the interaction between plant growth and soil temperatures during the first five weeks, they found no specific time within this period when the rate of growth was specially sensitive to temperature. Mederski and Jones (1963), using heating coils, obtained accelerated rates of development, increased dry matter production and grain yield. Beauchamp and Lathwell (1967a, 1967b) recognised that it was the increased rate of development associated with warmer soils that caused increased dry matter production during the early stages. (They also noted that plants at the same stage morphologically tended to be larger when grown at a lower temperature). Furthermore, they recognised that the apical meristem, the 'growing region' of the plant was below the soil surface during these early stages. Brouwer et al (1970) and Kleinendorst and Brouwer (1970) further investigated the effect of temperature on the shoot meristem and showed that this largely controlled shoot elongation. They ascribed differences in shoot expansion with root temperature to changes in root permeability to water, leading to partial water stress in the leaves. However, Watts (1971, 1972, 1973), in a series of experiments, using collars to vary meristem temperature independently of soil and air temperatures, showed that it was the direct effect of temperature on the meristem which largely controlled shoot extension. Changes of root permeability being less important.

It was thus recognised that the shoot meristem temperature was closely linked with the soil temperature during the early stages (up to the 8th leaf stage with the American hybrid used by Kleinendorst and Brouwer (1970) and more closely with the air temperature during the second half of vegetative development (Duncan et al, 1973), as the meristem rises above soil level. Adams and Thomson (1973) found that cooling the soil from 26° to 23°C affected stem temperature to a height of 60 cm, demonstrating that there must be an intermediate stage where the meristem temperature will be linked to both soil and air temperatures.

When experiments with soil warming have been carried through to plant maturity, the response of yield has varied. Fairbourn (1974) increased yield with a coal mulch; Miller (1968) found that grain yield was unaffected by glass- and water-filled polythene mulches. European mulching experiments have generally increased yields (Watts, 1970; Osafo and Milbourn, 1975; Phipps and Cockrane, 1975; Liakatas, 1978). However, in most situations when maize is grown in temperate climates it is entering the latter stages of growth in progressively deteriorating conditions. Daily insolation decreases after midsummer, and in the U.S. corn belt soil moisture levels decrease (the crop depending largely on stored soil water). Thus a hastening of development is advantageous by bringing these latter stages into more favourable conditions; (this will be discussed further in Section 1.3). In most of the experiments reported above, it is difficult to assess the factors limiting yield as comprehensive environmental records

are not presented. In contrast, tropical crops grow in radiation which does not vary so much throughout the year. At Kitale, lack of rainfall does not usually limit growth at any stage during the growing period. Few mulching or soil warming experiments have been done in the tropics, probably because soil temperatures are generally thought to be high enough, especially at lower altitudes (c.f. Kitale altitude 6,200 ft). Indeed, soil temperatures can exceed the optimum so that yield increases when the soil surface is kept cool with a crop residue mulch (Lal, 1974; Cooper and Law, 1978b).

It is difficult to relate published work on mulching to the environment of Kitale: the climate is fundamentally different, and so different factors will be limiting at different times. Moreover, in a study which is trying to relate early conditions to final yield, it is difficult to assess results without a comprehensive knowledge of conditions throughout the complete life of the plant.

2.2 Maize yield: Formation and Determination

2.2.1. Yield components.

In terms of quantitative analysis, there are three fundamental requirements for grain yield:

a) Grain sites (for assimilates to fill).

b) Assimilation of carbohydrates and translocation to grain sites.

c) Time, for grains to fill.

a) Grain site formation and viability

It is convenient to express grain number per unit area of land

as the product of a number of components:

$$N_t = N_p \times N_c \times N_g$$

where N_t = Total number of grains per unit area.

N_p = Number of plants per unit area.

N_c = Number of cobs per plant.

N_g - Number of grains per cob.

Maize, a gramineae, can tiller, but modern hybrids rarely do. Tillers tend to produce hermaphroditic heads with no husks which are especially susceptible to bird damage. To simplify matters further, one can assume the number of plants per unit area to be largely determined by the number of seeds sown under good agronomic conditions. The two most important components of grain number are thus number of cobs per plant and grains per cob.

The male inflorescence (tassel) forms at the stem apex, and female inflorescences (cobs) at leaf axils. The structure and development of both has been well documented by Bonnet (1966). Axillary buds are formed at the base of each leaf, except for the top few (about 6 in Kitale hybrids); these either remain vegetative (as do those at lower leaves) or become reproductive and form embryonic cobs. Spikelets usually arise on these cobs in characteristic double rows, each spikelet producing two florets, one of which is sterile. Thus one grain can form per spikelet. The topmost cob soon assumes apical dominance and a developmental hierarchy develops, the topmost one or two cobs developing fully (to produce grain), and lower cobs progressively less. The physiological and environmental factors that determine the number of cobs that will bear grain are little understood. This number is partly

a varietal characteristic, 'prolific' varieties producing several mature cobs per plant. However the number of grain-bearing ears seems to be inversely related to the maximum number of kernels per ear of the genotype, and selection has generally been in the direction of fewer and larger ears (Duncan, 1973).

Bonnet (1966) stated that both male and female inflorescences are indeterminate. Duncan (1973) observed that, if this were so, potential kernel number per ear (of a variety) would be expected to vary with environment, but this inference was not supported by his own observations. He also noted an inverse relation between kernels per row and number of rows, which tended to give a constant kernel number. In contrast, Carr and Milbourne (1976) state that recent work in Kenya suggests that number of florets formed is influenced by soil temperature. Now, if temperatures are sub-optimal during a developmental phase, then an increase in temperature will normally increase the rate of development and decrease the duration of that phase. Depending on whether rate or duration is most sensitive to temperature the maximum size of an organ (e.g. spikelet number) may increase or decrease. Such changes in spikelet number have been recorded in wheat (Owen, 1971; Halse and Weir, 1974), barley (Tingley et al, 1970), perennial ryegrass (Ryle, 1965) and rice (Yoshida, 1977). Such results usually come from growth room experiments as temperature effects are difficult to divorce from photoperiod effects in the field (Baker, pers. comm.). As floral apex development of wheat and barley occurs below ground level, soil temperature is expected to be the relevent variable. Lal (1974) stated that the number of ovules on the

embryonic ear shoots (of Nigerian varieties) is determined during the very early period of growth, whilst the growing point is still below the soil surface, but there seems to be no direct evidence for this statement. Otherwise, little work on temperature and spikelet number has been published for maize, possibly because of the difficulty of growing maize to maturity in controlled environments.

Once spikelets have been produced, the next possible block to further development is fertilization. Generally the silks are receptive during the time of pollen shed, although environmental stress may cause poor synchronisation, especially in hybrids of high uniformity. Also silks of 'tip' spikelets are last to develop and may not emerge in time. Daynard and Duncan (1969) used the presence of a black layer in the plancental region at maturity as indication of fertilization. They showed that many of the apparently undeveloped florets at the tip of a normal ear are fertilized but abort after limited development. Duncan (1973) stated that pollinated but undeveloped kernels were present on all the ears with undeveloped tip kernels that he examined. Pendleton and Hammond (1969) wrote that "the question of whether such grain abortion is controlled by total amount of daily photosynthate produced, or a specific hormone mechanism remains an agronomic challenge. An understanding of this abortion phenomena might .... lead to an exploitation of these potential grain sites". This statement is as relevent now as in 1969.

A number of shading, defoliation, thinning and water stress experiments have defined the time during which stress is most

likely to affect grain number. Generally this critical time extends from about two weeks before until about three weeks after silking. (Early et al, 1967; Wilson, 1968a; Claasen and Shaw, 1970b; Prine, 1971; Wilson and Allison, 1978a; Tollenaar and Daynard, 1978c). Tollenaar and Daynard found that the accumulation of dry matter in the tip kernels ceased at the onset of the linear period of grain growth.

Even though the importance of kernel abortion has been recognised, causes and mechanisms are still unknown. A recurring hypothesis is that light and assimilate supply to the kernels are the limiting factors (Prine, 1971; Wilson and Allison, 1978a), but there is no conclusive proof. Tollenaar and Daynard (1978b, 1978c) produce evidence both for and against this hypothesis. They also state that the role of a hormonal mechanism awaits investigation.

b) Carbohydrate production and translocation.

A much discussed question in the literature of crop physiology is whether yield is limited by the production capacity of the plant, or by the potential of the grains to accept the assimilate. If the 'source' were limiting, then either grain number would be varied during filling (by the stopping and starting of grain development), or final grain size would be correspondingly variable. If the 'sink' were wholly limiting, photosynthetic capacity during grain filling would be irrelevant, and yield would be determined solely by grain number. There is no evidence that grain number can be increased during filling, but grains may abort early in their development as discussed above. Grain size is obviously variable; but

there are limits. Very small grains would be less viable as seed and therefore ecologically undesirable. Common sense suggests that grain size cannot increase indefinitely. That the variability in grain size within a variety is small is shown by the stability of 1000 grain weight. Gallagher et al (1975) noted this for barley and work in Kenya (Cooper and Law, 1978b) shows similar behaviour by maize.

Duncan et al (1965) removed all the leaves from a number of corn plants, and covered the remainder of these plants with silver foil. They found that the kernel filling rate was similar to that of undefoliated plants, and largely dependent on temperature. This insensitivity to environmental factors other than temperature suggests relocation to the grain of assimilates from other parts of the plant, e.g. the stem. Many workers have now accepted the concept of a stem composed of insoluble structural tissues and a readily soluble storage fraction available for movement to the grain, and much work has revealed a decrease in stalk soluble solids (and/or sucrose), especially when the photosynthetic system is under stress (Van Reen and Singleton, 1952; Campbell, 1964; Duncan et al, 1965; Daynard et al, 1969; Hume and Campbell, 1972; Tollenaar and Daynard, 1978; Fairey and Daynard, 1978a, 1978b). Palmer et al (1973) also concluded that assimilation by leaves after flowering exceeded the capacity of kernels to accept carbon, suggesting that "cobs and husks may be the principal reservoirs of carbon that allow linear dry matter accumulation in kernels while the dry matter production of the plant fluctuates with daily radiation receipts".

Any discussion of source or sink limitations inevitably leads

to the conclusion of Evans (1973) that "source or sink?" is too polarised a question. Indeed, the two are interrelated in that it is quite conceivable, as we have seen above, that grain number (sink size) can be affected by assimilate availability (source size).

c) Duration of grain filling.

Grain filling is a developmental process where duration depends strongly on temperature. In most circumstances, duration is shortened by warmth. We have seen that the rate of kernel filling is also largely dependent on temperature, being faster at warmer temperatures. The interaction of these two factors, determining grain size, thus partially accounts for the conservative nature of grain size. Nevertheless, if either rate or duration is more tmperature sensitive than the other, grain size may be altered within the limits of it's plasticity.

Grain size has also been decreased by severe stress on the photosynthetic system during the period after grain number determination (Early et al, 1967; Wilson 1968a, 1968b; Claasen and Shaw, 1970b). As rate of filling is not greatly affected (see above) then it appears that such stresses could also shorten filling duration, presumably when too little stored carbohydrate is left to maintain grain growth.

2.2.2. Leaf production

So far we have considered an established crop. It is now pertinent to look at how conditions during earlier stages of development might affect crop growth and yield. We have seen that carbohydrate availability is a fundamental prerequisite for

good yield, both for filling the grain and probably by determining grain number. Good carbohydrate availability depends on three factors:

a) Sufficient leaf area to intercept practically all available solar radiation.

b) Efficient conversion of radiant energy by photosynthesis.

c) Development of this leaf area when seasonal insolation is strong, and when other environmental factors favour growth and development.

Each of these factors will be considered separately, although they interact in practice.

a) Leaf area

During the early stages of crop growth, the limiting factor for dry matter production is leaf area, which is sufficient to intercept only a fraction of the available solar radiation. With growth however, more solar radiation is absorbed by the crop; consequently growth during this period is approximately exponential and relative growth rate constant. As the crop develops further, new leaves tend to shade those already present, and relative growth rate falls. Eventually, if the plant population is sufficient, the foliage intercepts practically all the sunlight available, and production of more leaves will not increase light interception. Thus the absolute growth rate becomes more dependent on available light. In environments where daily radiation receipts and temperature are fairly constant, and water, nutrients etc. adequate, the absolute growth rate also tends to be constant and a linear phase of dry matter production ensues. The assumption here is that lower leaves are not parasitic - an assumption

shown to be reasonable by the work of McCree (1974). Maize crops in America (Ragland et al, 1965) and Kenya (Cooper and Law, 1977) exhibited such linear phases. The minimal leaf blade area index sufficient for about 95% light interception and linear growth is about 3 - 4 (Eik and Hanway, 1966; Williams et al, 1968).

b) Efficiency of the photosynthetic system.

Further consideration of the growth curves obtained by Cooper and Law (1977) suggests that even when ground cover is complete there may be differences in growth rates between different crops, and therefore in their photosynthetic efficiency. In one study (Cooper and Law, 1977) the differences were caused by time of planting, and the evidence suggests that soil temperature during the early stages is responsible. The way in which soil temperature can influence leaf efficiency, carbohydrate accumulation and possibly yield has been little investigated, is little understood and forms a major part of this thesis.

c) Timing of leaf area development.

In a constant environment, leaf area development rate would not be important per se, as long as sufficient foliage was present when necessary, during the yield determining phases. However, practically all parts of the world have changing seasons, and hence it is desirable to have sufficient leaf area present at a time of maximum solar radiation, sufficient water and optimum temperatures. However, as such matching has to fit the climatic requirements of earlier and later stages of the crop, a compromise has to be reached. For maize grown at Kitale the main climatic variable is rainfall, so that the crop is planted at the start of

the rainy season when sufficient water is available and matures before soils become too dry. Insolation varies relatively little throughout the year (Fig. 3.2) and so the compromise is small. In England by contrast, there is a marked variation of insolation throughout the year. Ideally, complete ground cover would be achieved, and yield determining phases would occur, when solar radiation is at a maximum. However, temperatures (especially soil temperatures) are low in the months preceeding June and so development of the maize crop is slow and sufficient leaf area does not develop until later, when insolation is falling. Thus maize in England ideally needs to be planted as soon as possible after soil temperatures are sufficient for growth to enable leaf area development as early as possible. Increasing this early developmental rate will then lead to an increased yield, as shown by mulching experiments in England (c.f. Section 2.1).

3. 1976 FIELD TRIALS

3.1 Effects of soil warming and seed size on growth and yield.

3.1.1. Introduction

The general aim of the work in the 1976 season was to investigate more fully the effects on late planted maize of early soil warming caused by a polythene mulch. The response to soil temperature of early plant size and final grain yield was described in Chapter 1. In a preliminary trial at Kitale by Law (unpublished), plant size during early growth was affected by seed size, but final yields were unaffected. Because of the similar initial effects of larger seeds and warmer soils it was decided to include seed size as a variable in this trial, to see how early plant size is related to final grain yield.

The specific objectives of the trial were:

a) To monitor the development of the vegetative apex, and to assess how leaf area is related both to early soil temperature and to seed size.

b) To monitor cob development and the initiation of spikelets and to discover whether these processes could be influenced by seed size and early soil temperature (either directly or indirectly).

c) To assess the importance, for grain yield determination, of plant size during the early stages of crop growth.

3.1.2. Materials and Methods.

Cooper and Law (1978b) gave a comprehensive description of the topography and soil type of the Trans-Nzoia District of Kenya.

Briefly, the soils in the area consist of well-drained dark reddish-brown to yellowish clays and sandy clay loams, having deep water tables which seldom rise within 10 m of the soil surface. They are easily managed but have a weak structure which can lead to capping, run-off and erosion. The site chosen for the 1976 experiments was cropped with hybrid maize in 1975.

The experiment was of the randomised block design, with four blocks of four treatments. These treatments were:

P - Medium seed, mulched for the period from planting to five weeks after emergence.

L - Large seed (1000 grain wt. - 649 g), unmulched.

M - Medium seed (432 g), unmulched.

S - Small grain (225 g), unmulched.

The experiment was laid out subdivided into two sections, each of two blocks, with continuity between the rows of adjacent plots within one of the sections (Fig. 3.1). Each plot consisted of three sample rows with one guard row on either side, giving two guard rows between the nearest sample rows of adjacent plots. Sample rows on the edge of each section were guarded by three rows. Each sample consisted of 20 plants: 2 adjacent plants were removed randomly from each of the three sample rows in plots within two of the blocks and from two of the sample rows of the remaining two blocks. The two sample rows which had no plants removed during a harvest were systematically rotated throughout the season to give an even depletion of plants from all the plots. Two guard plants were left on either side of the gap resulting from plants removed.

Figure 3.1 Experimental site 1976

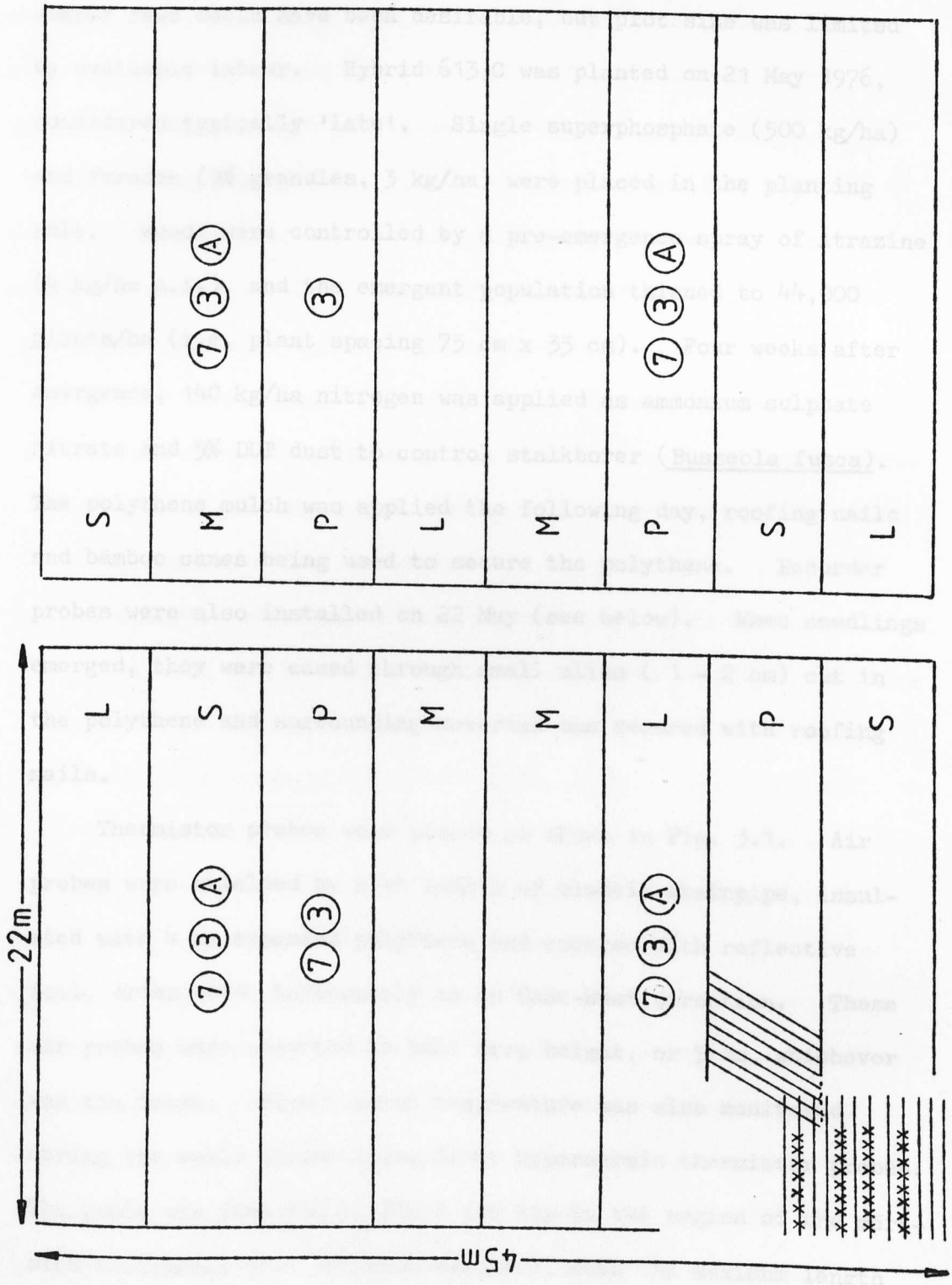
⑦ - thermistor probe at 7 cm depth, soil.

③ - " " " 3 cm " , "

Ⓐ - shielded thermistor probe, $\frac{1}{2}$ crop height.

——— - guard row

—xxxx— - sample row


S
M
P
L
M
P
S
L
⑦ ③ Ⓐ
③
⑦ ③ Ⓐ
22m
45m

This sampling procedure gave 400 plants, 20 samples of 20 plants each, from each treatment. More generous guarding of sample rows would have been desirable, but plot size was limited by available labour. Hybrid 613 C was planted on 21 May 1976, considered typically 'late'. Single superphosphate (500 kg/ha) and Furadan (5% granules, 3 kg/ha) were placed in the planting hole. Weeds were controlled by a pre-emergence spray of Atrazine (4 kg/ha a.i.), and the emergent population thinned to 44,000 plants/ha (i.e. plant spacing 75 cm x 35 cm). Four weeks after emergence, 140 kg/ha nitrogen was applied as ammonium sulphate nitrate and 5% DDT dust to control stalkborer (Busseola fusca). The polythene mulch was applied the following day, roofing nails and bamboo canes being used to secure the polythene. Recorder probes were also installed on 22 May (see below). When seedlings emerged, they were eased through small slits (1 - 2 cm) cut in the polythene and surrounding material was secured with roofing nails.

Thermistor probes were placed as shown in Fig. 3.1. Air probes were shielded by a 4" length of plastic drainpipe, insulated with 4 mm expanded polythene and covered with reflective foil, orientated horizontaly in an East-West direction. These air probes were adjusted to half crop height, or 5 cm, whichever was the least. Plant tissue temperature was also monitored during the early stages using Grant hyperdermic thermistor probes. The probe was inserted to place the tip in the region of the meristem (estimated from previous samples), with the maximum length possible within the plant to minimise conduction.

Plants were sampled at emergence, and subsequently every week during the morphological stages under investigation. During the early stages when the apical meristem was below ground level, care was taken to ensure all stem and leaf parts were removed. During the later stages plants were severed at ground level.

In the laboratory, the plants were washed and leaf appearance recorded (a leaf was considered 'appeared' when its tip emerged from the whorl). Subsamples for leaf and spikelet initiation analysis were taken as follows:

a) Leaf initiation: six plants were chosen with leaf appearance closest to the mean for that of the main sample. The plants were dissected under a microscope and visible leaf primordia number recorded.

b) Spikelet initiation: ten plants were chosen with size closest to the mean for that of the main sample. The cobs of this subsample were then dissected and the number of rows of spikelets and the number of spikelets per row recorded.

The plants from the total sample were then assessed for leaf area, using the method of Duncan and Hesketh (1968), with the individual leaf area of each leaf of each plant recorded. After tassel emergence, when the volume of material was substantial, subsamples of five plants of each treatment were measured by this method and their dry weight related to that of the remainder. The plants were then oven dried at 90°C for 48 - 72 hours and dry weights were recorded. Final harvest was taken when grains exhibited a black layer (Daynard and Duncan, 1969), and components of yield recorded.

3.1.3. Results

3.1.3.1. Climate, weather and environmental temperatures.

The long term monthly averages for solar radiation, mean air temperature and rainfall at Kitale are presented in Fig. 3.2. The weekly figures for the same variables during the growing season of 1976 are in Fig. 3.3.

Daily mean soil temperatures at 3 cm under bare soil and polythene, and air temperatures (half crop height) are presented in Fig. 3.4. Figures for bare soil are a mean of all three bare soil treatments as differences between these treatments were negligible. Daily mean soil temperature at 7 cm was within 0 - 0.5°C of the temperature at 3 cm, depending on whether there was a general warming or cooling trend, during that period. On a weekly basis however, these differences were negligible.

Figs. 3.3 and 3.4 show that above average insolation and below average rainfall during the first 2 - 3 weeks of June raised the temperature to between 21°C and 24°C under bare soil, and 26°C - 30°C under the polythene mulch. The soil temperatures during this period were in fact more typical of early planted maize than late planted. (Time of planting trials conducted at Kitale by Cooper and Law (1977) during 1976 showed that the mean soil temperature at 7.5 cm depth under early planted maize during the period from planting to the 12th leaf stage was 22.3°C, and that of the coolest late planting was 20.3°C.)

After the polythene mulch was removed (3 July) soil temperatures of the P treatment fell to levels similar to those in the unmulched plots. Indeed, soil temperatures under these previously mulched plots were slightly lower (0.5°C) for about a month

Figure 3.2 Long term averages for Solar radiation, Air temperature and Rainfall at Kitale (1890 m, 1°N 35°E).

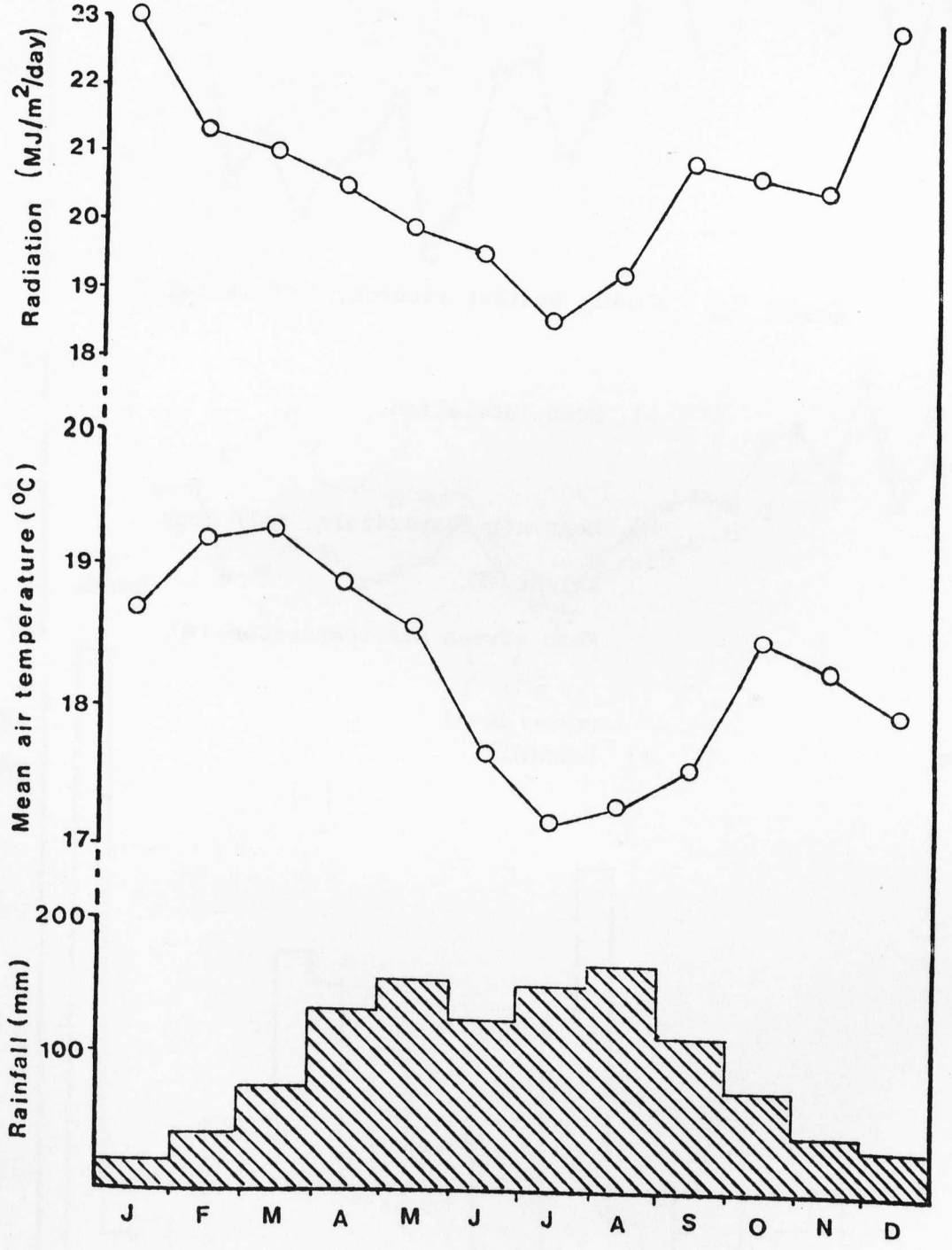

Radiation (MJ/m²/day)
23
22
21
20
19
18
Mean air temperature (°C)
20
19
18
17
Rainfall (mm)
200
100
J
F
M
A
M
J
J
A
S
O
N
D

Figure 3.3 Weekly weather records, 1976 (Kitale)

a) Mean insolation.

b) Mean air temperature, half crop height (□).
Mean screen air temperature (■).

c) Rainfall.

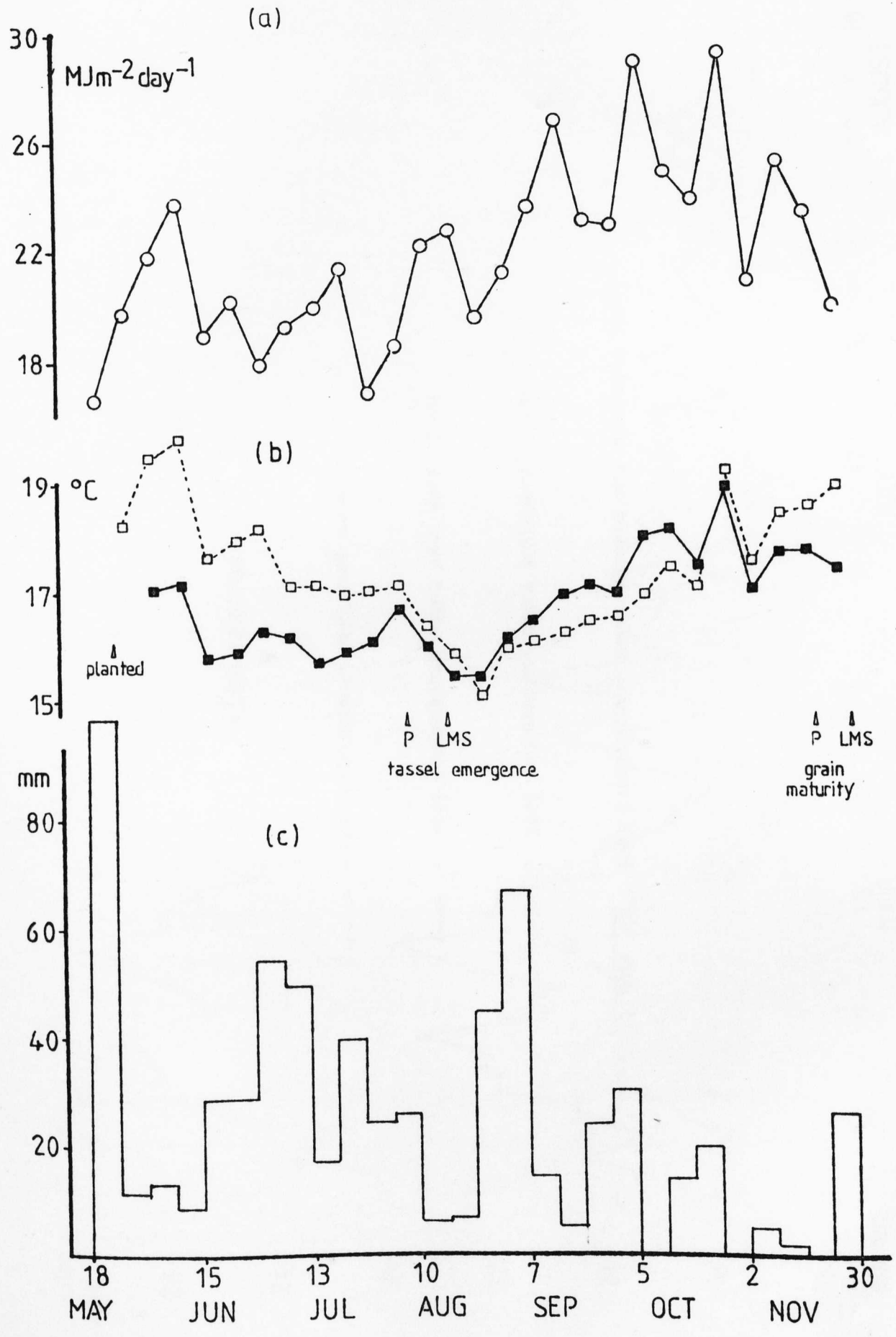
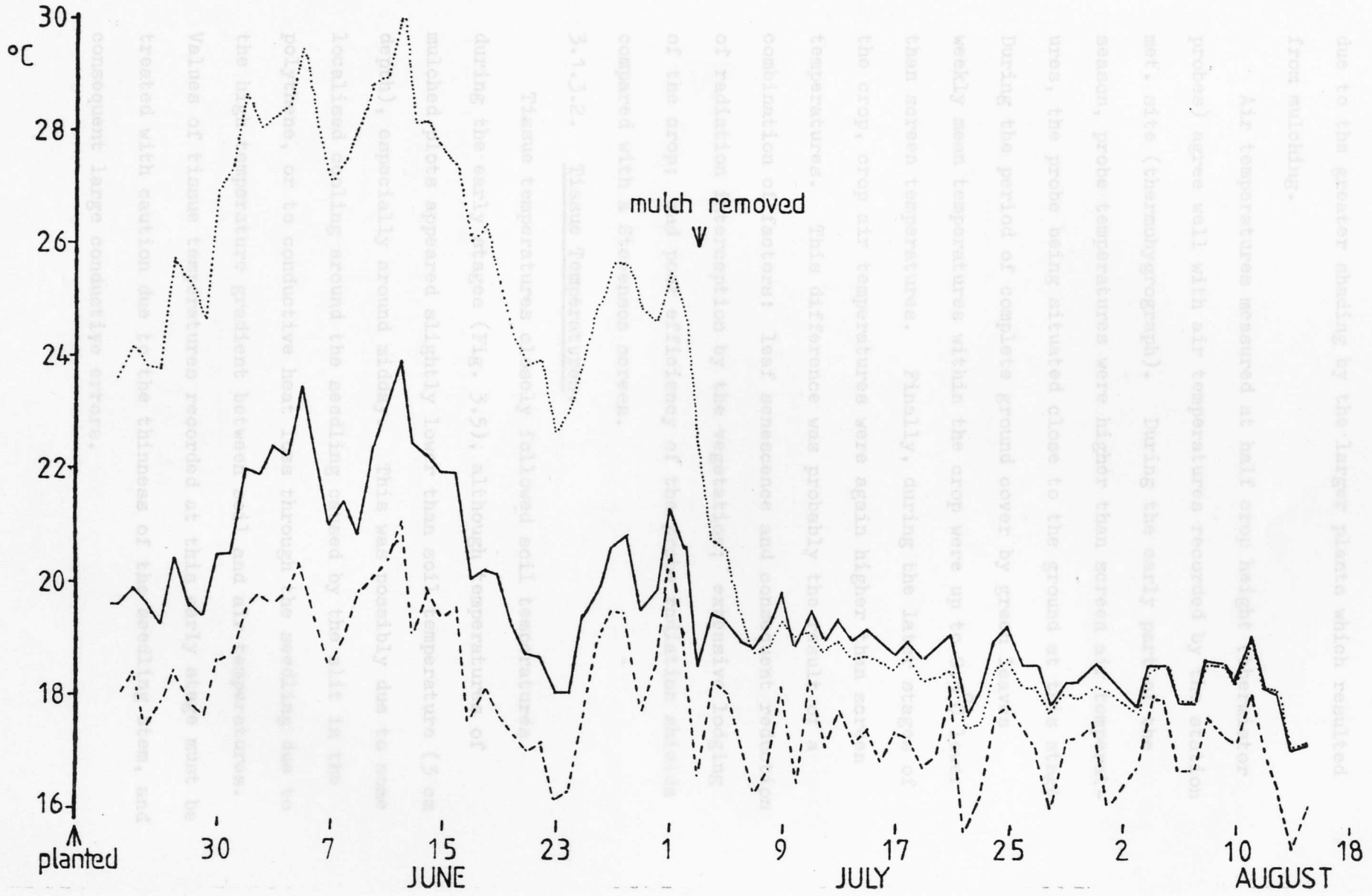

(a)
30
MJm⁻² day⁻¹
26
22
18
(b)
19
°C
17
15
planted
P
LMS
tassel emergence
P
LMS
grain maturity
mm
80
60
40
20
(c)
18 MAY
15 JUN
13 JUL
10 AUG
7 SEP
5 OCT
2 NOV
30

Figure 3.4 Soil temperatures under mulched and unmulched plots.

..... - soil temperature under polythene, 3 cm.

——— - soil temperature under bare soil, 3 cm.

- - - - - air temperature, half crop height.


30
°C
28
26
24
22
20
18
16
mulch removed
planted
30
7
15
23
1
9
17
25
2
10
18
JUNE
JULY
AUGUST

due to the greater shading by the larger plants which resulted from mulching.

Air temperatures measured at half crop height (thermistor probes) agree well with air temperatures recorded by the station met. site (thermohygrograph). During the early part of the season, probe temperatures were higher than screen air temperatures, the probe being situated close to the ground at this stage. During the period of complete ground cover by green leaves weekly mean temperatures within the crop were up to 0.5°C lower than screen temperatures. Finally, during the later stages of the crop, crop air temperatures were again higher than screen temperatures. This difference was probably the result of a combination of factors: leaf senescence and consequent reduction of radiation interception by the vegetation; extensive lodging of the crop; and poor efficiency of the probe radiation shields compared with a Stevenson screen.

3.1.3.2. Tissue Temperatures.

Tissue temperatures closely followed soil temperatures during the early stages (Fig. 3.5), although temperatures of mulched plots appeared slightly lower than soil temperature (3 cm depth), especially around midday. This was possibly due to some localised cooling around the seedling caused by the slit in the polythene, or to conductive heat loss through the seedling due to the high temperature gradient between soil and air temperatures. Values of tissue temperatures recorded at this early stage must be treated with caution due to the thinness of the seedling stem, and consequent large conductive errors.

Figure 3.5 Plant meristem temperatures, 2/6/76.

a) Soil temperature (3 cm) under polythene (- - - - - - -).
Soil temperature (3 cm) under bare soil (.....).
Air temperature, half crop height (————).

b) Difference between soil temperature and meristem temperature of mulched (- - - -) and unmulched (.....) plants.

c) Difference between air temperature and meristem temperature of mulched (- - - -) and unmulched (.....) plants.

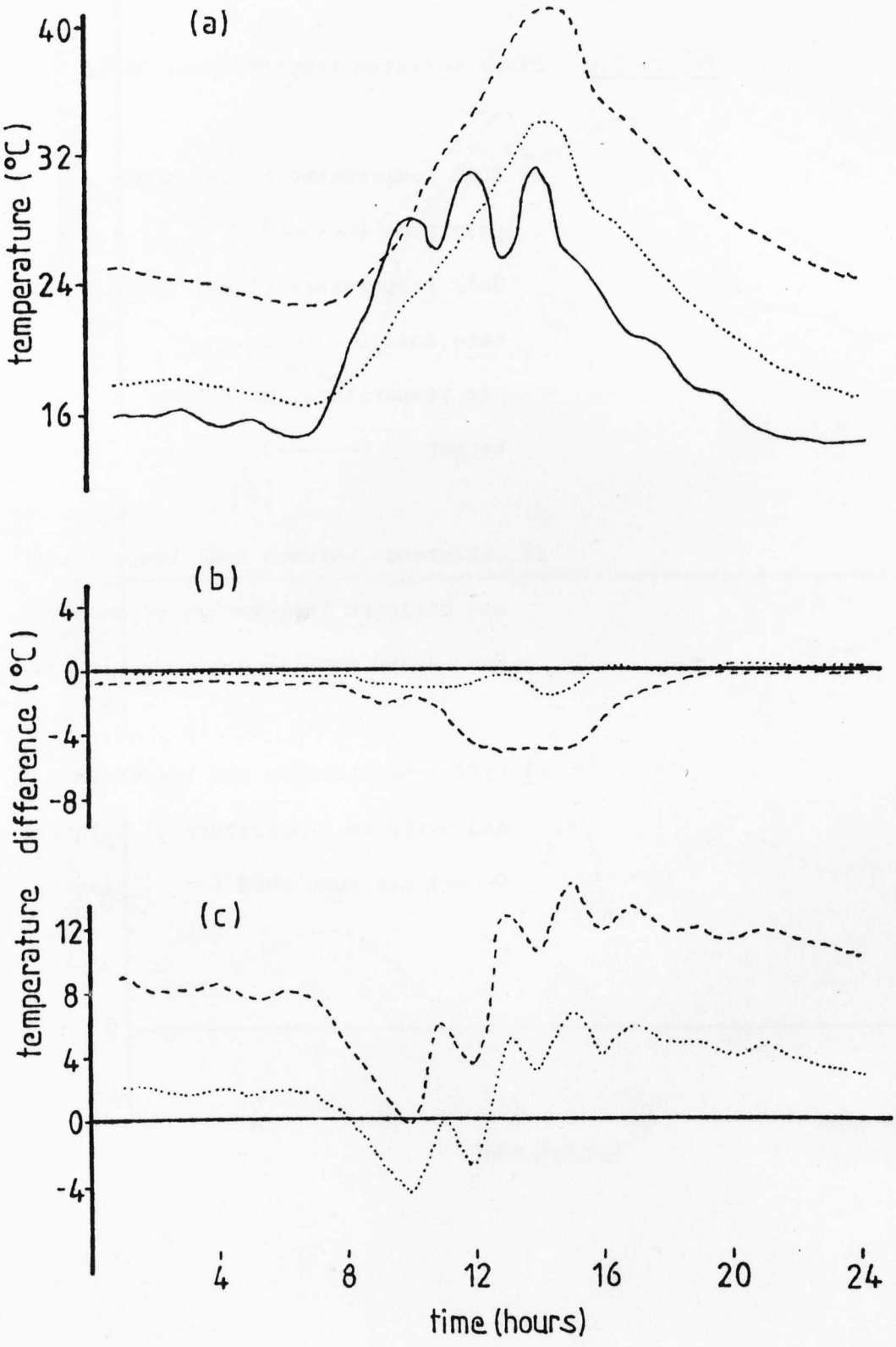

(a)
40
32
24
16
temperature (°C)
(b)
4
0
-4
-8
difference (°C)
(c)
12
8
4
0
-4
temperature
4
8
12
16
20
24
time (hours)

Figure 3.6 Plant meristem temperatures, 16/6/76.

a) Soil temperature (3 cm) under polythene (- - - - -).
Soil temperature (3 cm) under bare soil (.....).
Air temperature, half crop height (———).

b) Difference between soil temperature and meristem temperature of mulched (- - -) and unmulched (.....) plants.

c) Difference between air temperature and meristem temperature of mulched (- - - -) and unmulched (.....) plants.

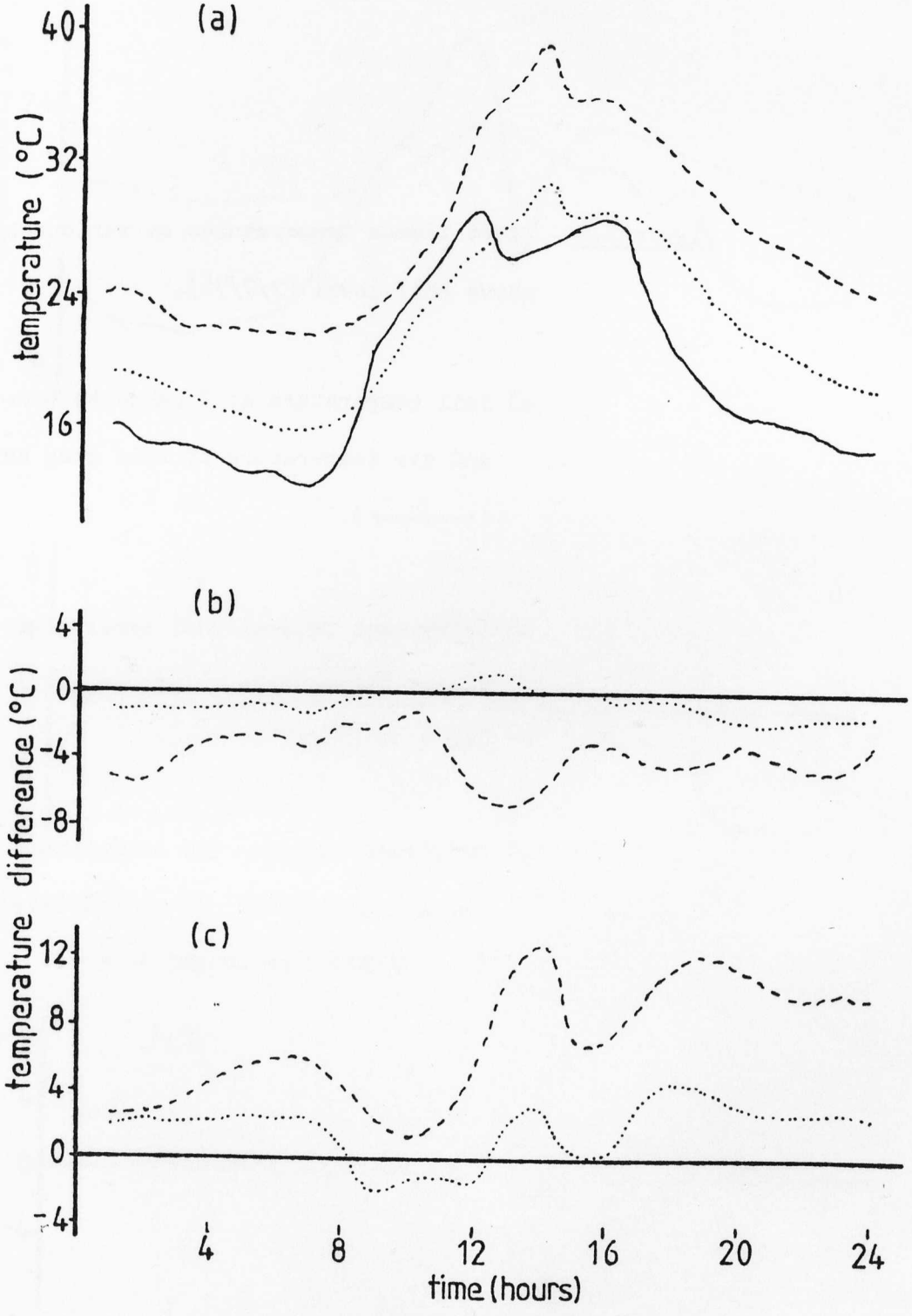

(a)
40
32
24
16
temperature (°C)
(b)
4
0
-4
-8
difference (°C)
(c)
12
8
4
0
-4
temperature
4
8
12
16
20
24
time (hours)

Figure 3.7 Plant tissue temperatures at various heights above soil level (7/7/76).

a) Soil temperature at 3 cm depth (- - - - - -) and air temperature at half crop height (————).

b) Difference between soil temperature and tissue temperature at ground level (.....) and 7 cm height (- - - -).

c) Difference between air temperature and tissue temperature at ground level (.....) and 7 cm height (- - - -).

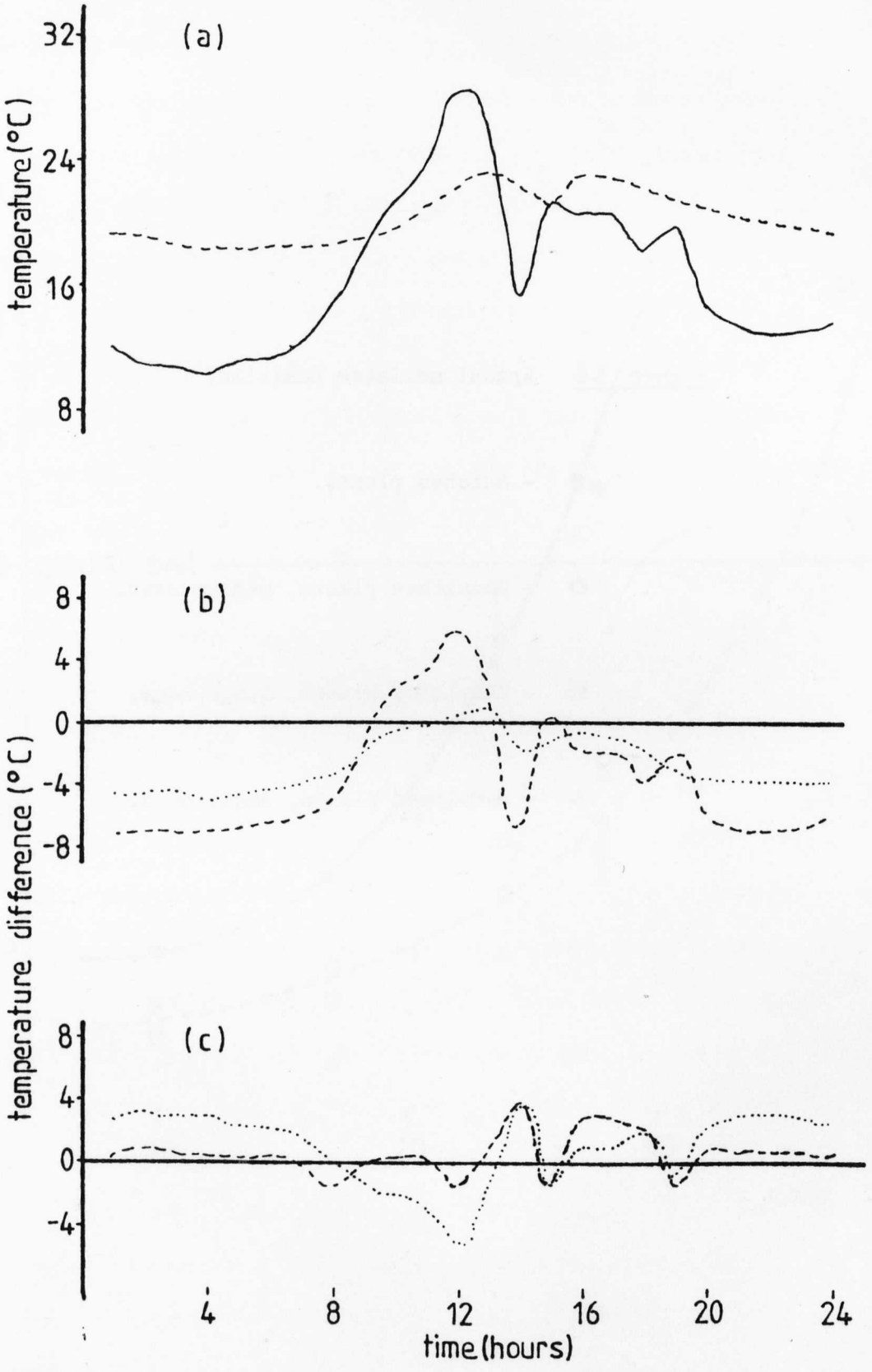

(a)
32
24
16
8
temperature (°C)
(b)
8
4
0
-4
-8
temperature difference (°C)
(c)
8
4
0
-4
4
8
12
16
20
24
time (hours)

Figure 3.8 Apical meristem position.

● - Mulched plants.

○ - Unmulched plants, medium seed.

□ - Unmulched plants, large seed.

△ - Unmulched plants, small seed.

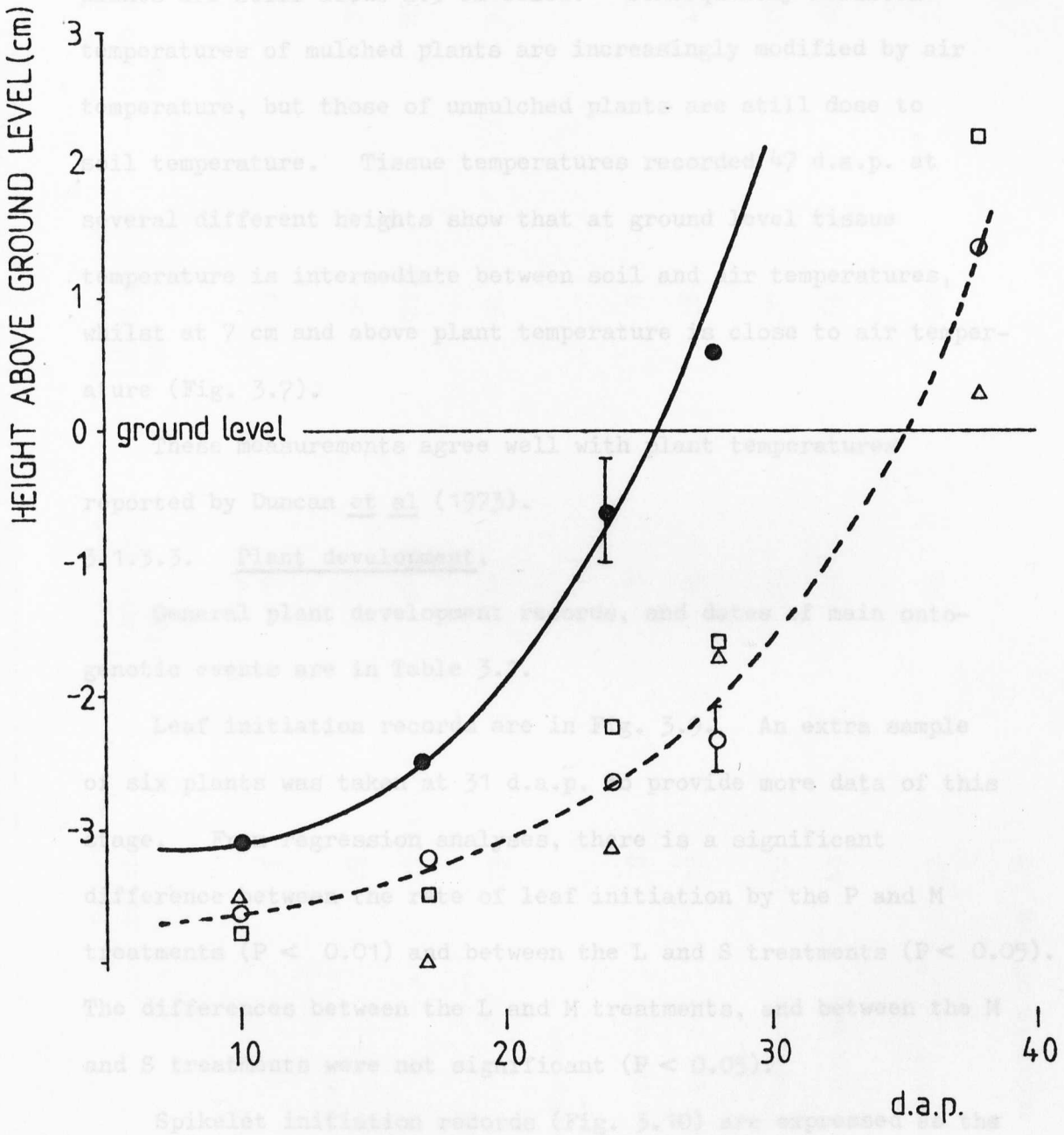

HEIGHT ABOVE GROUND LEVEL(cm)
3
2
1
0
-1
-2
-3
ground level
10
20
30
40
d.a.p.

Fig. 3.6 shows tissue temperatures recorded 26 days after planting (d.a.p.). The apical meristem of mulched plants is approximately at ground level (Fig. 3.8), but those of unmulched plants are still about 2.5 cm below. Consequently meristem temperatures of mulched plants are increasingly modified by air temperature, but those of unmulched plants are still dose to soil temperature. Tissue temperatures recorded 47 d.a.p. at several different heights show that at ground level tissue temperature is intermediate between soil and air temperatures, whilst at 7 cm and above plant temperature is close to air temperature (Fig. 3.7).

These measurements agree well with plant temperatures reported by Duncan et al (1973).

3.1.3.3. Plant development.

General plant development records, and dates of main ontogenetic events are in Table 3.1.

Leaf initiation records are in Fig. 3.9. An extra sample of six plants was taken at 31 d.a.p. to provide more data of this stage. From regression analyses, there is a significant difference between the rate of leaf initiation by the P and M treatments ($P < 0.01$) and between the L and S treatments ($P < 0.05$). The differences between the L and M treatments, and between the M and S treatments were not significant ($P < 0.05$).

Spikelet initiation records (Fig. 3.10) are expressed as the number of spikelets initiated within one row on the 1st and 2nd cobs. Spikelet production on the second cob followed that of the 1st cob, but about three days later. The pattern of production

Table 3.1. Effect of soil warming and seed size on plant development.

Treatment		Polythene mulch	Large seed (1000 gr.wt 649)	Medium seed (1000 gr.wt. 432	Small seed (1000 gr.wt. 225)
Days planting - 75% emergence		7	9	9	9
Days planting - tassel initiation*		29	32	34	37
Leaf Number		25.1(0.1)	24.2	23.7	23.9
Days planting - 50% tassel emergence		79	90	91	93
Days 50% tassel emergence - 50% silk emergence -					
	1st cob	8	8	7	7
	2nd cob	32	20	18	14
% final silk emergence	1st cob	100	100	100	100
	2nd cob	45	55	66	65
Days 50% tassel emergence - black layer (grain maturity)		93	93	93	93

* From graphical analysis of Fig 3.9

Figure 3.9 Leaf initiation.

 - Mulched plants

 - Unmulched plants, large seed

 - Unmulched plants, medium seed

 - Unmulched plants, small seed

(arrows denote extrapolated dates of tassel initiation)

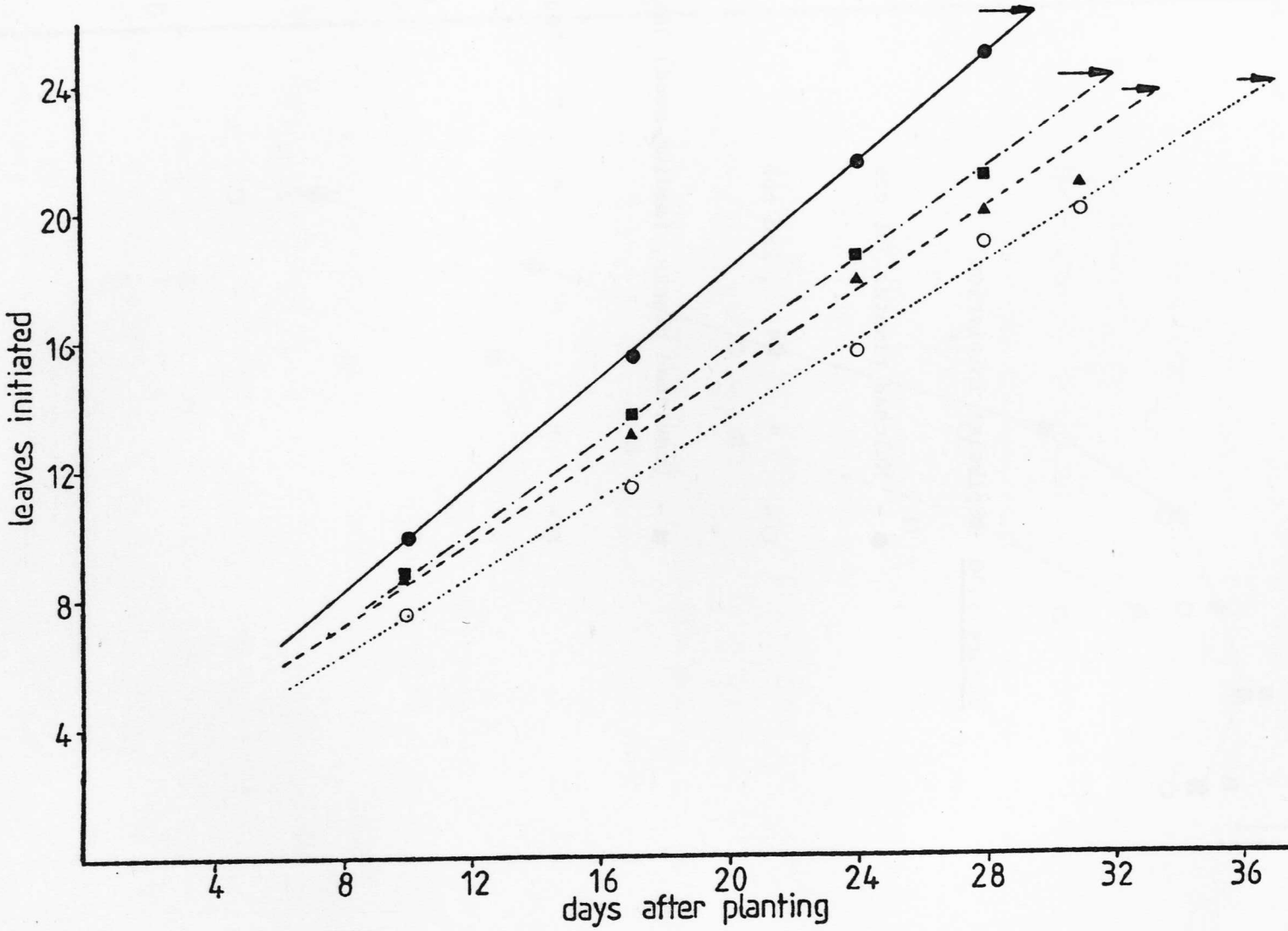

leaves initiated
4
8
12
16
20
24
4
8
12
16
20
24
28
32
36
days after planting

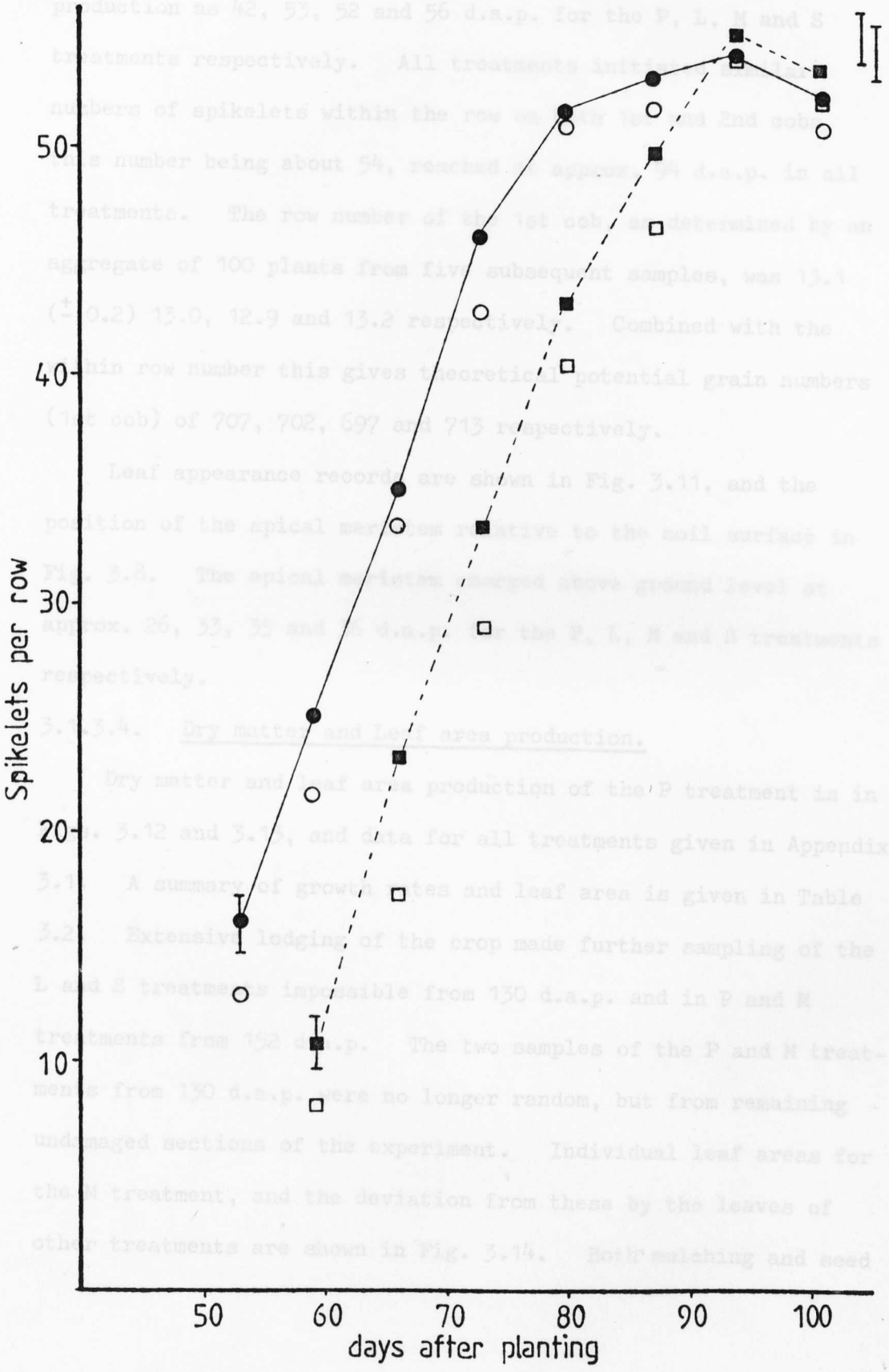
Figure 3.10 Spikelet initiation

● - Mulched plants, 1st cob

○ - " " , 2nd cob

■ - Unmulched plants, (medium seed) 1st cob.

□ - " " " " 2nd cob.


Spikelets per row
10
20
30
40
50
50
60
70
80
90
100
days after planting

was similar for all treatments, but the timing different. Extrapolation gives the theoretical dates of the start of spikelet production as 42, 53, 52 and 56 d.a.p. for the P, L, M and S treatments respectively. All treatments initiated similar numbers of spikelets within the row on both 1st and 2nd cobs, this number being about 54, reached at approx. 94 d.a.p. in all treatments. The row number of the 1st cob, as determined by an aggregate of 100 plants from five subsequent samples, was 13.1 ($\pm$ 0.2) 13.0, 12.9 and 13.2 respectively. Combined with the within row number this gives theoretical potential grain numbers (1st cob) of 707, 702, 697 and 713 respectively.

Leaf appearance records are shown in Fig. 3.11, and the position of the apical meristem relative to the soil surface in Fig. 3.8. The apical meristem emerged above ground level at approx. 26, 33, 35 and 36 d.a.p. for the P, L, M and S treatments respectively.

3.1.3.4. Dry matter and Leaf area production.

Dry matter and leaf area production of the P treatment is in Figs. 3.12 and 3.13, and data for all treatments given in Appendix 3.1. A summary of growth rates and leaf area is given in Table 3.2. Extensive lodging of the crop made further sampling of the L and S treatments impossible from 130 d.a.p. and in P and M treatments from 152 d.a.p. The two samples of the P and M treatments from 130 d.a.p. were no longer random, but from remaining undamaged sections of the experiment. Individual leaf areas for the M treatment, and the deviation from these by the leaves of other treatments are shown in Fig. 3.14. Both mulching and seed

Figure 3.11 Leaf appearance

● - Mulched plants

○ - Unmulched plants, medium seed.

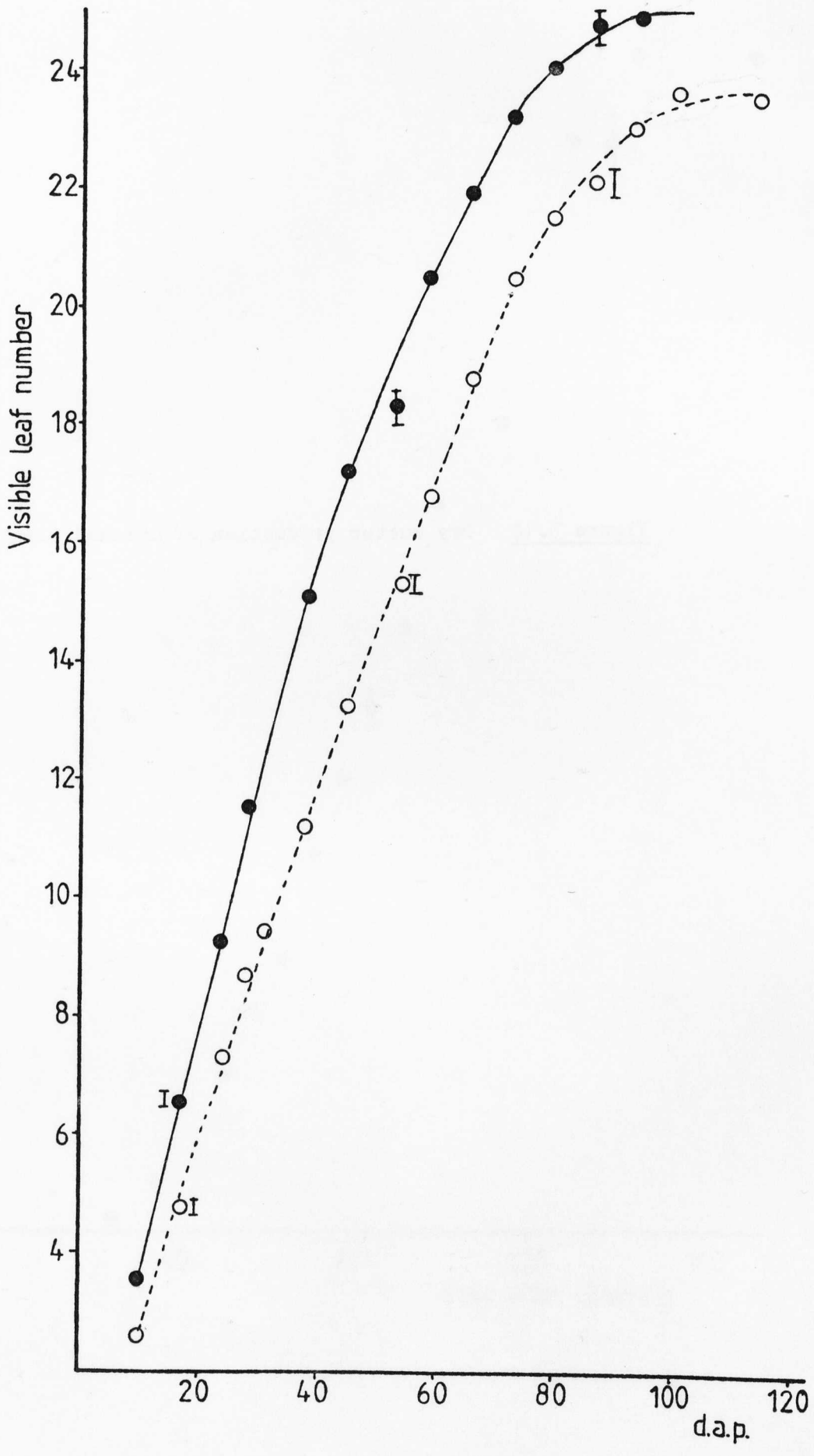

Visible leaf number
24
22
20
18
16
14
12
10
8
6
4
20
40
60
80
100
120
d.a.p.

Figure 3.12 Dry matter production of mulched plants.

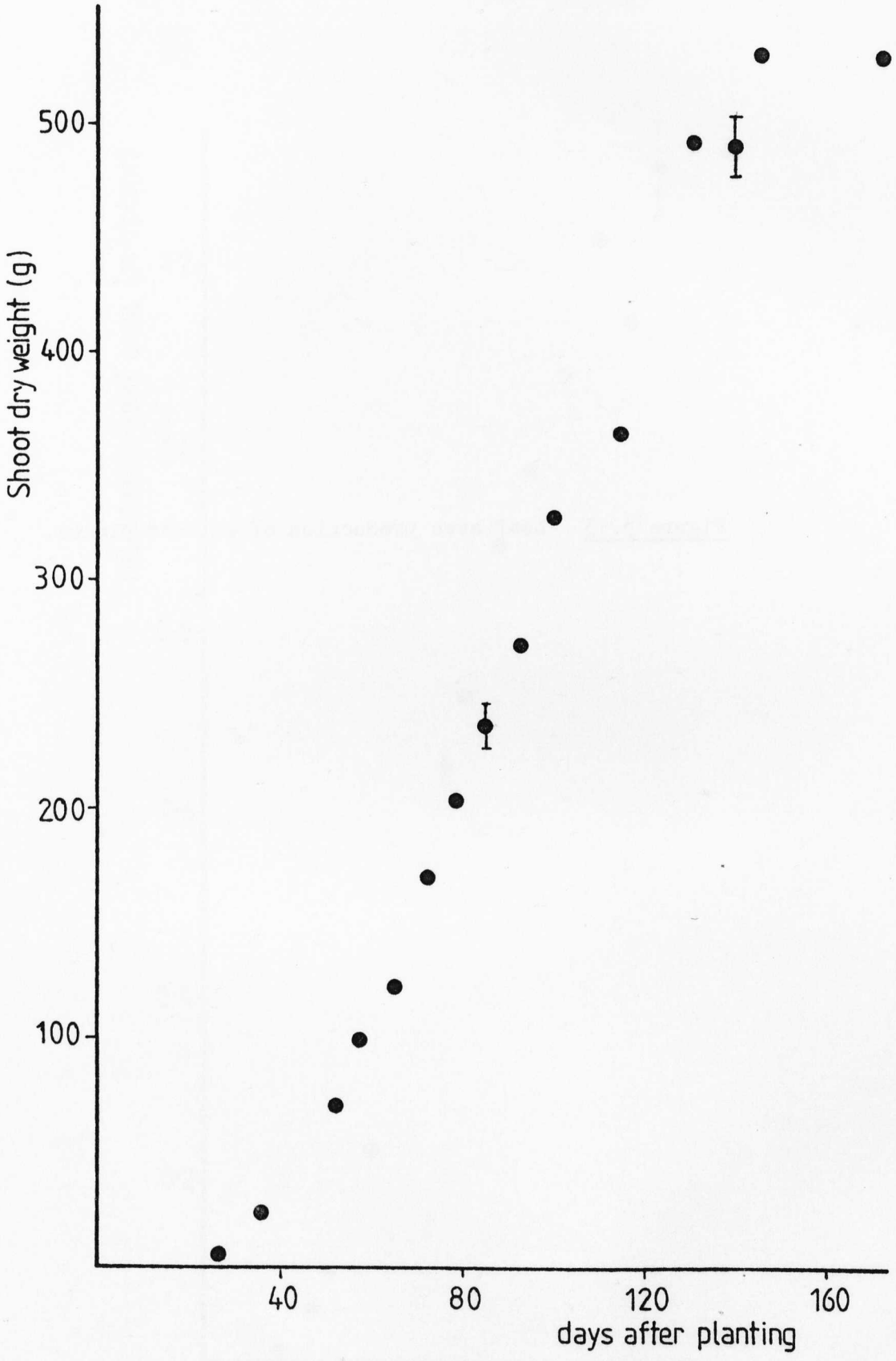

Shoot dry weight (g)
500
400
300
200
100
40
80
120
160
days after planting

Figure 3.13 Leaf area production of mulched plants.

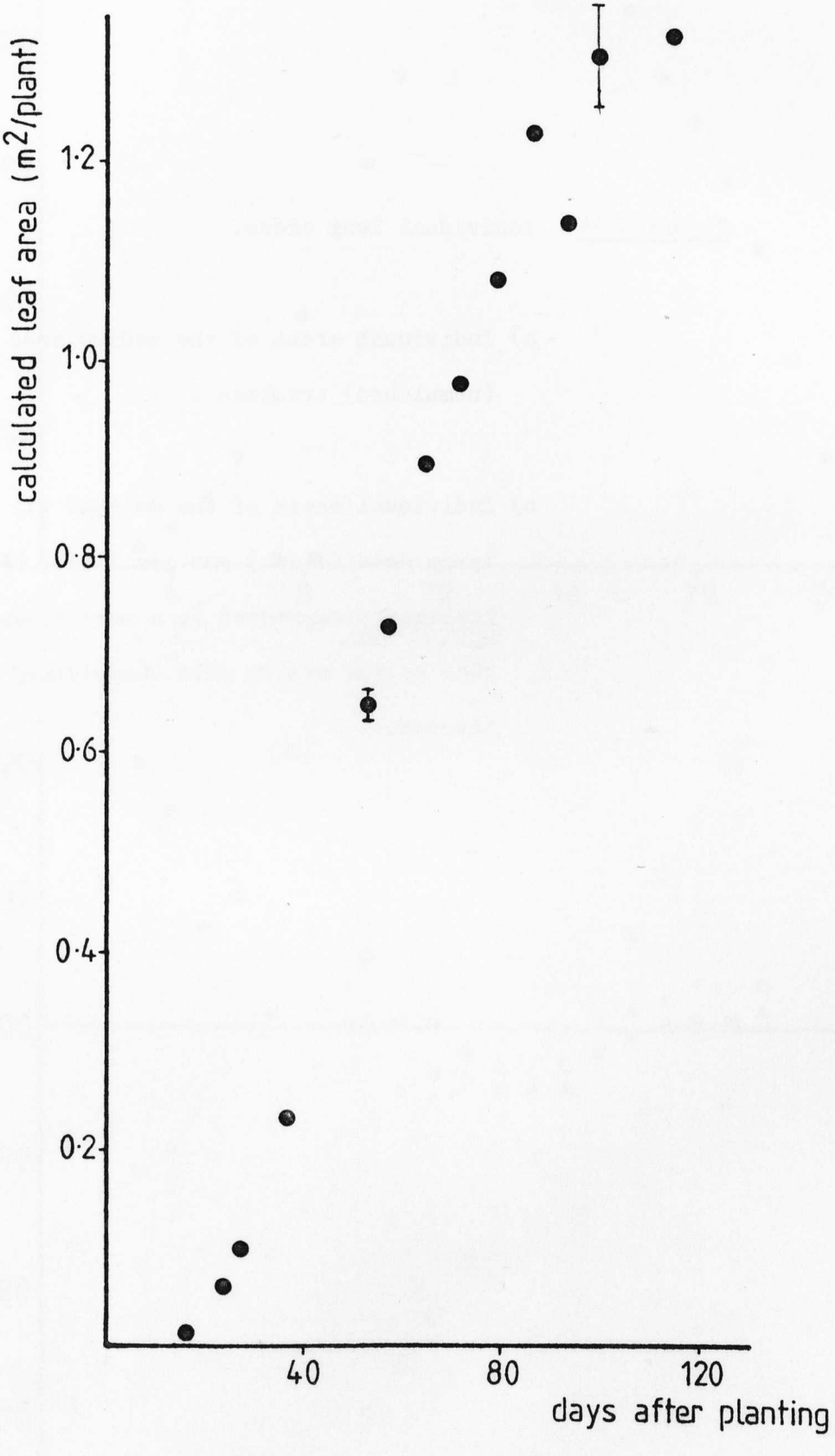
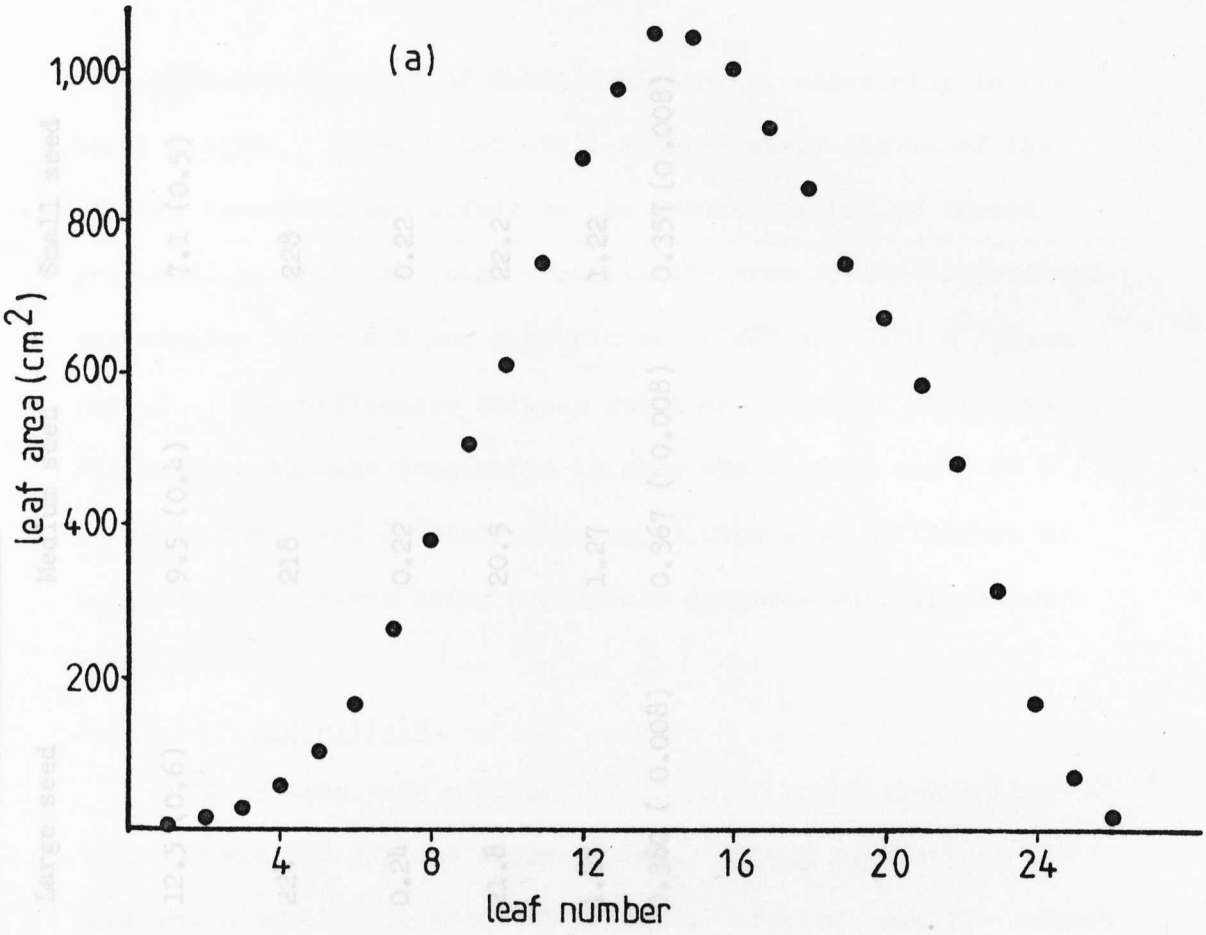

calculated leaf area (m^2/plant)
1·2
1·0
0·8
0·6
0·4
0·2
40
80
120
days after planting

Figure 3.14 Individual leaf areas.

a) Individual areas of the medium seed (unmulched) treatment.

b) Individual areas of the mulched (○ ○) large seed (■ ■) and small seed (▲ ▲) treatments expressed as a percentage of that of the medium seed (unmulched) treatment.


(a)
1,000
800
600
400
200
leaf area (cm²)
4
8
12
16
20
24
leaf number

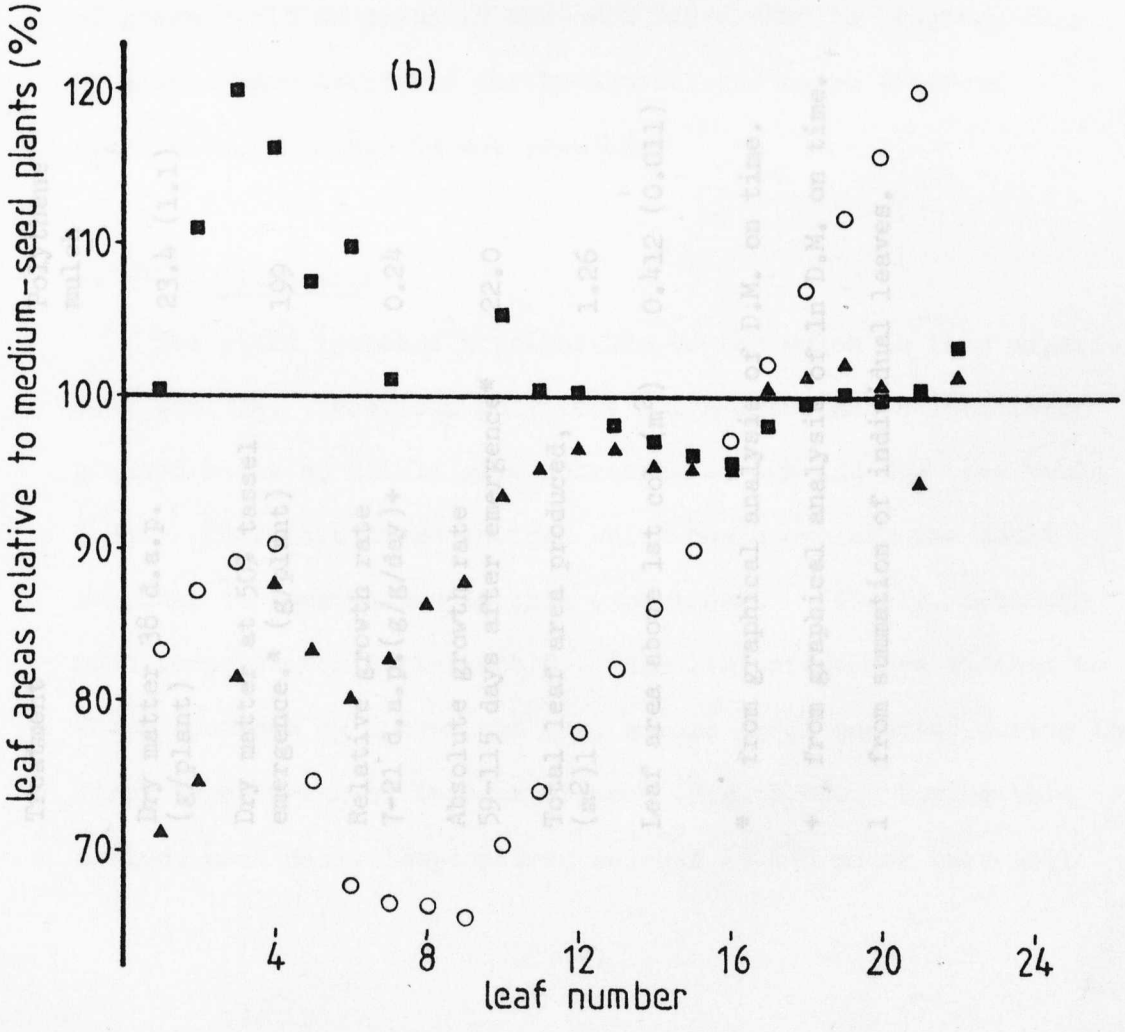

(b)
120
110
100
90
80
70
leaf areas relative to medium-seed plants (%)
4
8
12
16
20
24
leaf number

Table 3.2. Dry matter and leaf area production.

Treatment	Polythene mulch	Large seed	Medium seed	Small seed
Dry matter 38 d.a.p. (g/plant)	23.4 (1.1)	12.5 (0.6)	9.5 (0.4)	7.1 (0.5)
Dry matter at 50% tassel emergence.* (g/plant)	199	224	218	228
Relative growth rate 7-21 d.a.p.(g/g/day)+	0.24	0.24	0.22	0.22
Absolute growth rate 59-115 days after emergence*	22.0	21.8	20.5	22.2
Total leaf area produced, (m^2)1	1.26	1.27	1.27	1.22
Leaf area above 1st cob (m^2)	0.412 (0.011)	0.380 (0.008)	0.367 (0.008)	0.357 (0 .008)

* from graphical analysis of D.M. on time.

\+ from graphical analysis of ln D.M. on time.

1 from summation of individual leaves.

size affected the size of individual leaves, especially in the early stages. However the small area of early leaves of the mulched treatment was offset by the greater number of leaves produced, so that the total accumulative area of leaves produced was similar for the P and M treatments (1.25 and 1.26 m^2/plant resp.). The difference between total accumulative leaf area of different seed size treatments is also small (1.27 and 1.24 m^2/ plant in the L and S treatments resp.), the size difference of early smaller leaves being negligible compared with the larger later leaves.

3.1.3.5. Grain yield.

Grain yields were similar for the L, M and S treatments: 159, 159 and 168 g/plant respectively. Yield of the P treatment was slightly higher: 180 g/plant. A more complete summary of grain yield is given in Appendix 3.2. Due to lodging, only 60 plants were harvested per treatment, and hence rigorous statistical analysis is not possible.

3.1.4. Discussion

The yield increase attributable to the mulch in this experiment was 13%. Previous polythene mulch experiments with late planted maize at Kitale gave increases of 60% and 30% (see Table 3.3). There are three factors which could explain the small response to temperature in this experiment. Firstly, although mean temperatures during the 0 - 12th leaf stage were similar to those recorded by Cooper and Law, a warm spell occurred during the first three weeks of this experiment (Fig. 3.4). During this period, mean daily temperatures reached 23.8°C under bare soil

and 30°C under mulched soil.

Table 3.3

Year	1975*		1976*		1976	
	mulch	control	mulch	control	mulch	control
Planting date	1/6/75	1/6/75	10/5/76	10/5/76	21/5/76	21/5/76
Mean soil temp, planting emergence °C	25.8	20.4	26.4	21.2	24.4	19.8
Mean soil temp, 0-12 visible leaves °C	27.3	21.2	26.9	21.9	27.5	20.9
Grain yield, g/plant	213	133	238	172	202	179

* From Cooper & Law (1978b)

Note - all yields quoted at 12.5% moisture content.

Soil temperatures of 38°C and 44°C were recorded at 3 cm depth under unmulched and mulched soils. Polythene mulch trials by Cooper and Law (1978a) have shown that most of the response to soil warming occurs during the first three weeks after planting. The warm spell also occurred during the 0 - 12 leaf stage in the 1976 trial of Cooper and Law, but it occurred during the period 3 - 5 weeks after planting, when temperature would be less important. Thus it is conceivable that during the period of maximum response, bare soil temperatures during this experiment were nearly optimal for final yield, whereas temperatures under the mulch may have exceeded the optimum.

Secondly, temperatures recorded by Cooper and Law (1978b)

were calculated from readings taken twice daily, at 7 am. and 2 pm., using a relationship between these and two-hourly recordings from previous experiments. In view of the apparent critical nature of one or two degrees rise in temperature, comparison of temperatures measured by the two different methods may not be valid.

Thirdly, the extensive lodging during grain fill may have been selective. Mulched plants had an increased resistance to lodging, apparently because they were slightly smaller and stouter. Indeed few plants from the P treatment lodged. If yield was related to lodging resistance in some way, then the final yield sample of unmulched plants may have been biased towards higher yields.

As there was no substantial yield increases due to the mulch, it is difficult to identify the physiological factors through which changes in early soil temperature may modify yield. However, a number of points are evident.

The mulch altered the rate and duration of leaf initiation, resulting in a higher final leaf number in the mulched treatment. This finding agrees with the leaf number and soil temperature observations of Cooper (1978b). It suggests that the base temperature for the rate of leaf initiation may be slightly higher than that for the duration. Accurate calculation of these base temperatures is difficult due to small temperature variation during this period (consequently only two points are available - from mulched and unmulched plots). The considered effects of the mulch on leaf number and leaf size was to produce a cumulative leaf area similar

to that of unmulched plants. This suggests that the yield benefits of warmer soils are not mediated through a larger leaf area. The pattern of dry matter accumulation suggests that no further advantage is gained by an increase in leaf area from about 60 d.a.p., at which stage the plant has a leaf area of about 0.8 m^2 (equivalent to an LAI of 3.5). It would be a poor crop of maize which did not exceed this leaf area at Kitale. During the later stages of the crop, the differences between the leaf area in the mulched and unmulched plots became minimal, both in terms of leaf area above the cob (Table 3.2) and total leaf area remaining. Although senescence was not recorded in 1976, it appeared that more of the early leaves senesced on the mulched treatment to leave about the same effective area during grain filling. Because of the unsubstantiated nature of this point it was decided to investigate leaf area more thoroughly in 1977.

Spikelet initiation began when the embryonic cob apices were well above soil level. From the tissue temperatures measured in this experiment, and those by Duncan et al (1973), the temperature of the developing cobs at this time is closely related to air temperatures. Air temperatures change very little during the part of the year relevant to the time of planting effect, i.e. June - Sept. (Fig. 3.2) and varied little during spikelet initiation during the experiment. Furthermore the period during which early soil temperature is related to yield is also well before the period of spikelet initiation. Thus from a consideration of the position and timing of cob development, one would expect to find little change in spikelet production rate or duration, or potential grain

number, mediated by a change of temperature caused by early soil warming. This conclusion for Kenya Highland maize is not comparable with the statement by Lal (1974) that 'the number of ovules on the embryonic ear shoots is determined during the very early period of growth, whilst the growing point is still below the soil surface'.

Previous work at Kitale (Law & Cooper, 1976; Cooper & Law, 1977), suggested that larger plants would more fully realise the genetic yield potential than smaller ones. Later mulch trials, however (Cooper & Law, 1978b) showed that yield can increase when there is no difference in total dry weight at tasselling, and this experiment shows that plant size in the early stages (either on a time or on a developmental scale) is not always related to final grain yield. It therefore seems that the size of the plant at tasselling or earlier is not important *per se*. Empirical relations cited in Chapter I do not relate cause and effect, but suggest that early plant size and final grain yield are both related to soil temperature. Time of planting trials show that warmer soils are associated with increased growth rate (under conditions of full crop cover) and higher yields. Furthermore, in the work reported here, crop growth rates and yields were similar for different seed sizes. It is therefore pertinent to consider rates of growth during the season and to relate them to final yield, rather than absolute sizes at any point. Unfortunately plot sizes during the mulching trials reported by Cooper and Law (1978) made destructive sampling impossible. Data from the mulched and unmulched plots in this experiment appear to show

little difference in growth rates, but the limitations of the data already discussed make conclusions about the relation of yield to crop growth rate tenuous. For this reason it was decided to investigate this aspect further in 1977.

3.2. Effects of plant population on growth and yield, 1976.

3.2.1. Introduction.

A simple and convenient means of altering grain yield per plant is to change the population density. It was decided to plant an experiment at two contrasting populations to investigate the relation between growth rate, kernel number formation and yield.

2.2.2. Materials and Methods.

The experiment was of the randomised block design, with six blocks of two treatments each. The two populations were 111,000 plants/ha (30 cm x 30 cm spacing) and 17,800 plants/ha (75 cm x 75 cm). Normal recommended spacing for this cultivar (H613C) is 44,000 plants/ha. The trial was planted on 9 April 1976 with all agronomic practices except plant population similar to those described in Section 3.1.2. Fertilizer rates were the same on a per plant basis. Sampling was done randomly from four of the blocks with two blocks left for final harvests. Plants were sampled in groups of five from the high population, with two guard rows between sample rows, in pairs from the low population with one guard row between sample rows. Each sample consisted of 20 plants (sub-sample of six for spikelet measurements) and was conducted as in Section 3.1.2. with the following measurements

taken:

a) Leaf appearance.

b) Leaf area.

c) Spikelet initiation.

d) Total dry weight.

3.2.3. Results

Sampling records before 29 July 1976 are presented in Appendix 3.3. No later sampling was done, due to severe lodging, especially in the high population. There was little difference between growth rate of the two treatments until about 35 days after planting and thereafter the plant growth rate of the higher population was substantially less than in the wider spacing. This difference was reflected by the rate of leaf area production which followed a similar pattern during this period, although proportionately the decrease was not so marked as that of dry matter accumulation. Leaf appearance rate remained unaffected until about 40 days after planting, when it was decreased slightly in the higher spacing.

Although measurements of spikelet number were variable due to the small sub-sample used, the rate of spikelet production and final spikelet number, appeared to be unaffected, even though population pressure at this time resulted in a much slower rate of plant growth. This agrees with findings by Wilson and Allison (1978b). Yields per plant were about five times greater in the low population than in the high population, caused mainly by an increased grain number. More complete measurements of yield are given in Appendix 3.4. Again, detailed statistical

analysis is not possible, as 20 plants were selected from sections of the experiment still standing. However, yield differences are large enough for certain inferences to be made.

3.2.4. Discussion.

Within the limits of this experiment, yield per plant increased as population decreased, largely because of increased grain number. Furthermore an increase of assimilate supply per plant was not associated with the production of more potential grain sites, but with the ability of more of these potential sites to develop into mature grains. Kernel weight was also reduced in the higher population showing that even though a smaller number of grains developed, there was still not enough photosynthate to fill them, due to the smaller leaf area and to less light reaching individual plants in the denser canopy. Also smaller, thin stemmed plants, as in the higher population, would presumably have reduced carbohydrate reserves to draw upon.

3.3. Conclusions from 1976 field trials.

The measurements provide strong evidence for the following conclusions:

1) Warmer soils do not induce larger leaf areas, and larger leaf areas do not increase crop growth rate of typical Kitale maize crops (early or late planted).
2) Spikelet production is not affected by plant size or growth rate, and is not a major discriminant of yield in time of planting or mulching studies.
3) Plant size per se at any stage is not a discriminant of yield.
4) Seed size is not correlated with final grain yield.

4. 1977 FIELD TRIALS

4.1 Introduction

Because the differences of yield observed in 1976 were small, a further mulching trial was conducted in 1977. To minimise the risk of encountering a warm spell during the important early stages of growth, three times of planting were chosen. With this arrangement it was also possible to investigate the interaction of time of planting and mulch effects.

Late planted maize exhibits a lower crop growth rate during the linear phase of growth, (Cooper and Law, 1977). This behaviour implies either that leaf and canopy photosynthesis is reduced or that growth capacity is reduced. (Soil temperature has been found to influence the production of hormones by maize roots - Atkin et al, 1973).) To investigate the hypothesis that the source of assimilate may be altered by soil temperature, it was decided to determine leaf nitrogen content which is often related to leaf photosynthetic efficiency (Ryle and Hesketh, 1969; Natr, 1972). To investigate the possibility that growth was "sink" limited, soluble carbohydrate status was also monitored (a method suggested by Duncan, 1973).

To reduce the probability of lodging, hybrid 6302 was used instead of H613C because it has a higher lodging resistance and its parental lines are similar to those of H613C (Darrah, pers. comm.) similar physiological interactions with the environment would be expected.

The main aims of the 1977 investigation were thus:

a) To substantiate the conclusions from the 1976 experi-

ment that leaf and spikelet initiation are not major discriminants of yield.

b) To determine whether yield was correlated with growth rate (during the linear phase) and to investigate possible causes of the relatively slow rates of growth characteristic of late planted maize.

4.2 Materials and Methods

For each time of planting, there was one mulched (polythene) and one unmulched treatment. The six treatments were thus:

a) UM1 - Early planting, unmulched) planted when the rainy
b) M1 - " " , mulched) season was judged to have begun.

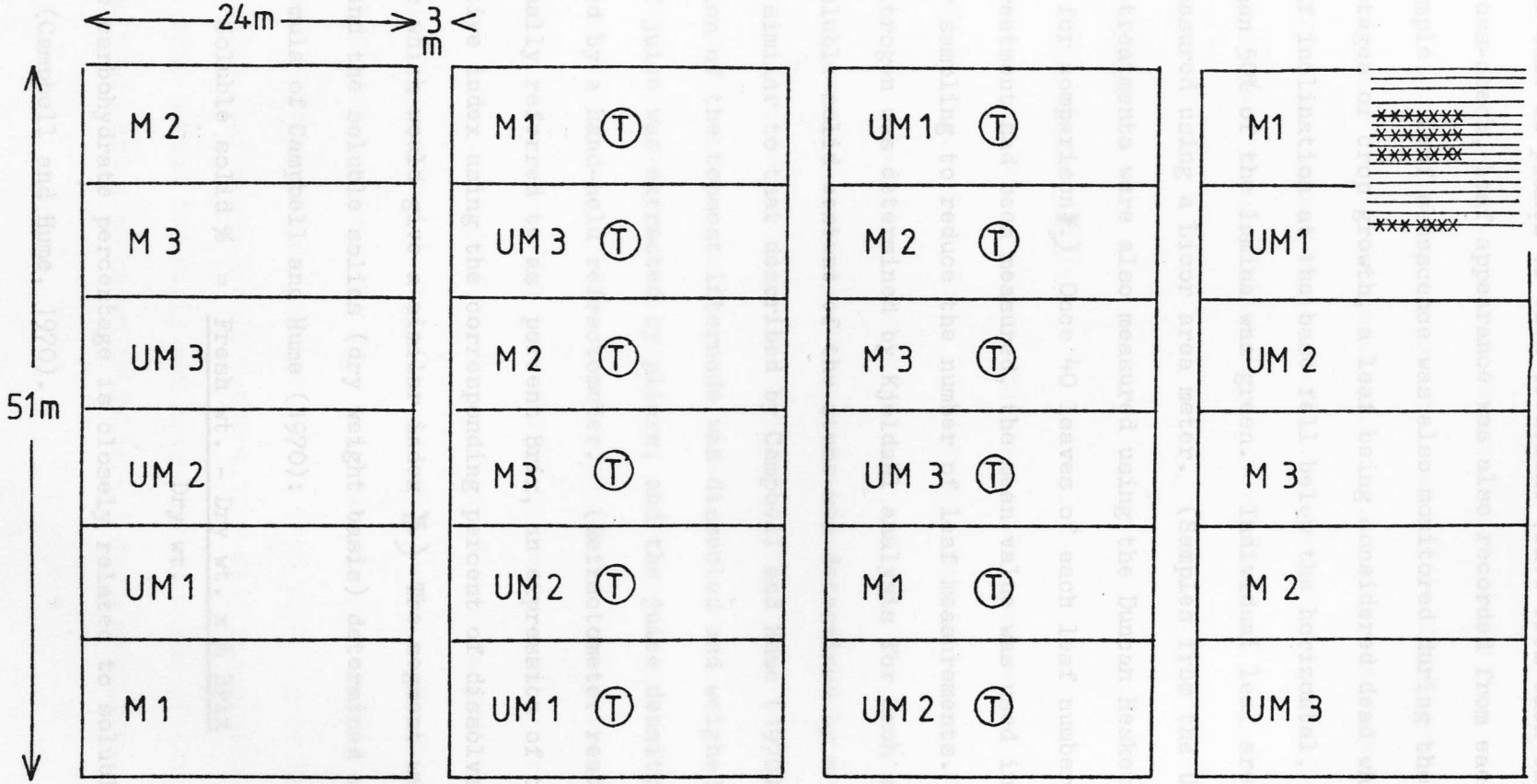
c) UM2 - Intermediate planting, unmulched.

d) M2 - " " " mulched.

e) UM3 - Late planted, unmulched) judged to be the latest
f) M3 - " " , mulched) planting possible without risk of water deficits during later stages.

Crop husbandry was described in Section 3.1.2., and Fig. 4.1 shows the plot layout. Soil temperature (7 cm depth) and air temperature (at half crop height) were monitored on each plot in the two central blocks. Twenty plants from each treatment were sampled approximately every 10 days, five adjacent plots being taken randomly from within one of the three sample rows of each plot. (The sample row was rotated systematically.) Three guard plants were left between each site of removal and five guard plants at the end of each sample row. Final harvest was designated as five groups of five plants from each plot.

Figure 4.1 Experimental site 1977



To reduce sample variability, leaf appearance was recorded from the same 20 plants of each treatment (five from each block). As a cross-check, leaf appearance was also recorded from each main sample. Leaf senescence was also monitored during the later stages of crop growth, a leaf being considered dead when the leaf inclination at the base fell below the horizontal, or less than 50% of the lamina was green. Individual leaf areas were measured using a Licor area meter. (Samples from the UM1 and M1 treatments were also measured using the Duncan Hesketh method for comparison). Once 40 leaves of each leaf number for each treatment had been measured, the mean value was used in further sampling to reduce the number of leaf measurements. Leaf nitrogen was determined by Kjeldahl analysis for each sample.

Soluble solid content of the stems was determined by a method similar to that described by Campbell and Hume (1970). A section of the topmost internode was dissected and weighed. A drop of juice was extracted by pliers, and the juice density was measured by a hand-held refractometer. (Refractometer readings are usually referred to as percent Brix, an expression of the refractive index using the corresponding percent of dissolved sucrose which would give a similar index). The segment was dried and the soluble solids (dry weight basis) determined using the formula of Campbell and Hume (1970):

$$\text{Soluble solid \%} = \frac{\text{Fresh wt.} - \text{Dry wt.} \times \text{\% Brix}}{\text{Dry wt.}}$$

Soluble carbohydrate percentage is closely related to soluble solids (Campbell and Hume, 1970).

Spikelet initiation was determined by the method described in Section 3.1.2. In addition the number of embryos judged to be still developing was counted during the grain-filling period.

Plant dry weight (by components) was recorded and mean kernel weight determined from the mean grain number and mean grain weight of the samples. Yield components were recorded when the kernels reached black layer formation.

4.3. Results

4.3.1. The weather 1977.

Rainfall, solar radiation and screen air temperature are presented in Fig. 4.2. Until 20 September rainfall records come from the trial site; later records are from the Research Station Meteorological Site (because field records were destroyed by fire). Screen air temperature and radiation were recorded at the Met. Site, about 1 km from the trial.

Early soil temperatures, from the three times of planting are shown in Fig. 4.3. Direct measurements for the period 13 - 20 May were unavailable due to recorder failure. Date for this period was calculated from the regression of soil temperature on screen air temperature (weekly means) which was the most highly correlated variable from the Met. Site records ($r = 0.96$). The mean soil temperatures during the period from planting to the 12th visible leaf stage are in Table 4.1. Soil temperatures during the same period for early and late planted maize of three previous years are also shown in Table 4.1 for comparison.

Figure 4.2 Weekly mean insolation, air temperature and rainfall, (1977).

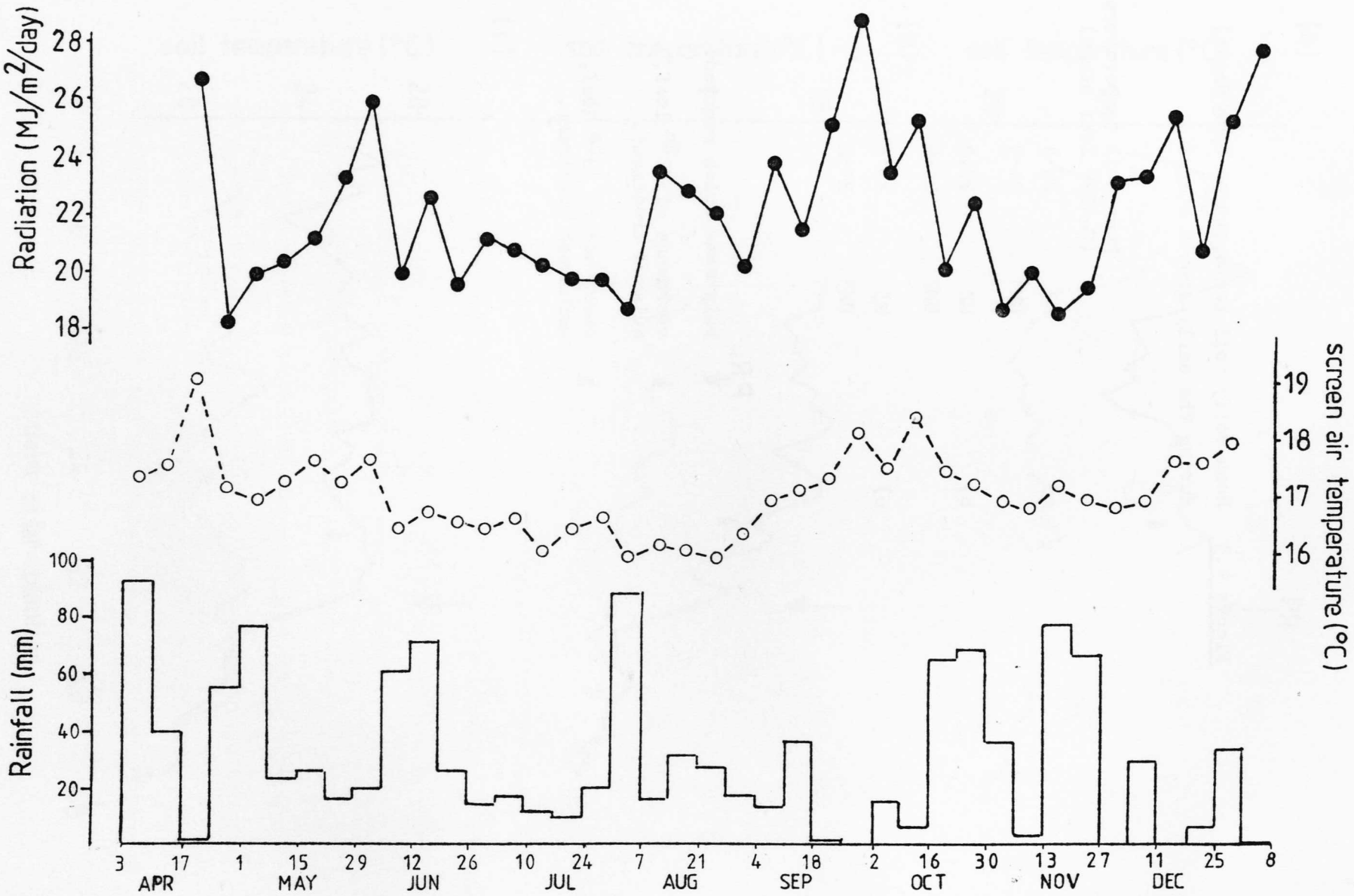

Radiation (MJ/m²/day)
28
26
24
22
20
18
screen air temperature (°C)
19
18
17
16
Rainfall (mm)
100
80
60
40
20
3 17 1 15 29 12 26 10 24 7 21 4 18 2 16 30 13 27 11 25 8
APR MAY JUN JUL AUG SEP OCT NOV DEC

Figure 4.3 Mean daily soil temperatures (3cm depth) during the early growth stages.

		Mean soil temperature (0-12th leaf stage)
a)	M1	26·4
	UM1	21·9
b)	M2	27·2
	UM2	21·6
c)	M3	25·5
	UM3	21·2

PR ↓ polythene mulch removed.

▮ emergence of 12th leaf, mulched treatment.

▮ emergence of 12th leaf, unmulched treatment.

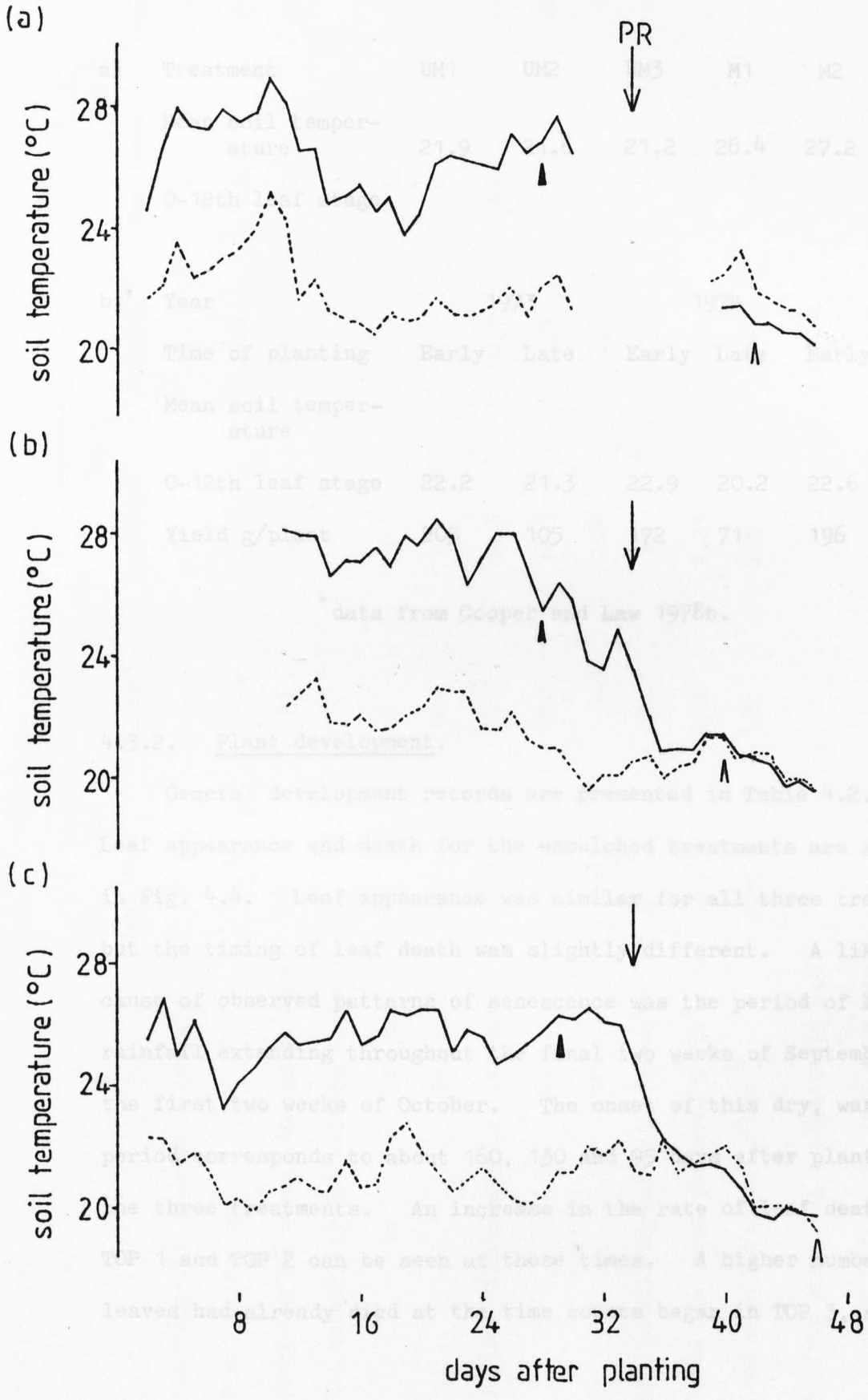

(a)
PR
soil temperature (°C)
28
24
20
(b)
soil temperature (°C)
28
24
20
(c)
soil temperature (°C)
28
24
20
8
16
24
32
40
48
days after planting

Table 4.1. Soil temperatures during early growth.

a)

Treatment	UM1	UM2	UM3	M1	M2	M3
Mean soil temperature 0-12th leaf stage	21.9	21.6	21.2	26.4	27.2	25.5

b)*

Year	1973		1974		1975	
Time of planting	Early	Late	Early	Late	Early	Late
Mean soil temperature 0-12th leaf stage	22.2	21.3	22.9	20.2	22.6	19.2
Yield g/plant	205	105	172	71	196	48

*data from Cooper and Law 1978b.

4.3.2. Plant development.

General development records are presented in Table 4.2. Leaf appearance and death for the unmulched treatments are shown in Fig. 4.4. Leaf appearance was similar for all three treatments but the timing of leaf death was slightly different. A likely cause of observed patterns of senescence was the period of low rainfall extending throughout the final two weeks of September and the first two weeks of October. The onset of this dry, warm period corresponds to about 160, 130 and 95 days after planting in the three treatments. An increase in the rate of leaf death in TOP 1 and TOP 2 can be seen at these times. A higher number of leaves had already died at the time counts began in TOP 3, and the

Table 4.2.

Plant Development

	Top 1		Top 2		Top 3	
	Unmulched	Mulched	Unmulched	Mulched	Unmulched	Mulched
Planting- 75% emergence (days)	10	6	8	6	9	6
Final leaf number	23.0	24.8	23.9	25.2	23.0	24.9
Planting-50% tassel emergence(days)	99	88	101	90	105	93
50% tasselling-50% silking (days)						
1st cob	8	6	9	7	11	6
2nd cob	24	14	-	-	-	-
% final silk emergence 1st cob	99.7	99.7	99.3	99.7	98.8	99.7
2nd cob	58.1	62.5	74.3	76.3	27.0	44.6
3rd cob	1.0	1.4	2.4	1.6	0.0	0.3
50% tasselling-maturity (days)*	88	90	85	83	88	84
Total leaf area produced m^2/pl^+	1.26	1.26	1.25	1.25	1.08	1.13
Leaf area duration m^2Day^a	129	137	118	119	104	105

* from graphical analysis fig 4.9

\+ sum of individual leaf area means

a from leaf area curves

Figure 4.4 Leaf appearance.

a) UM1

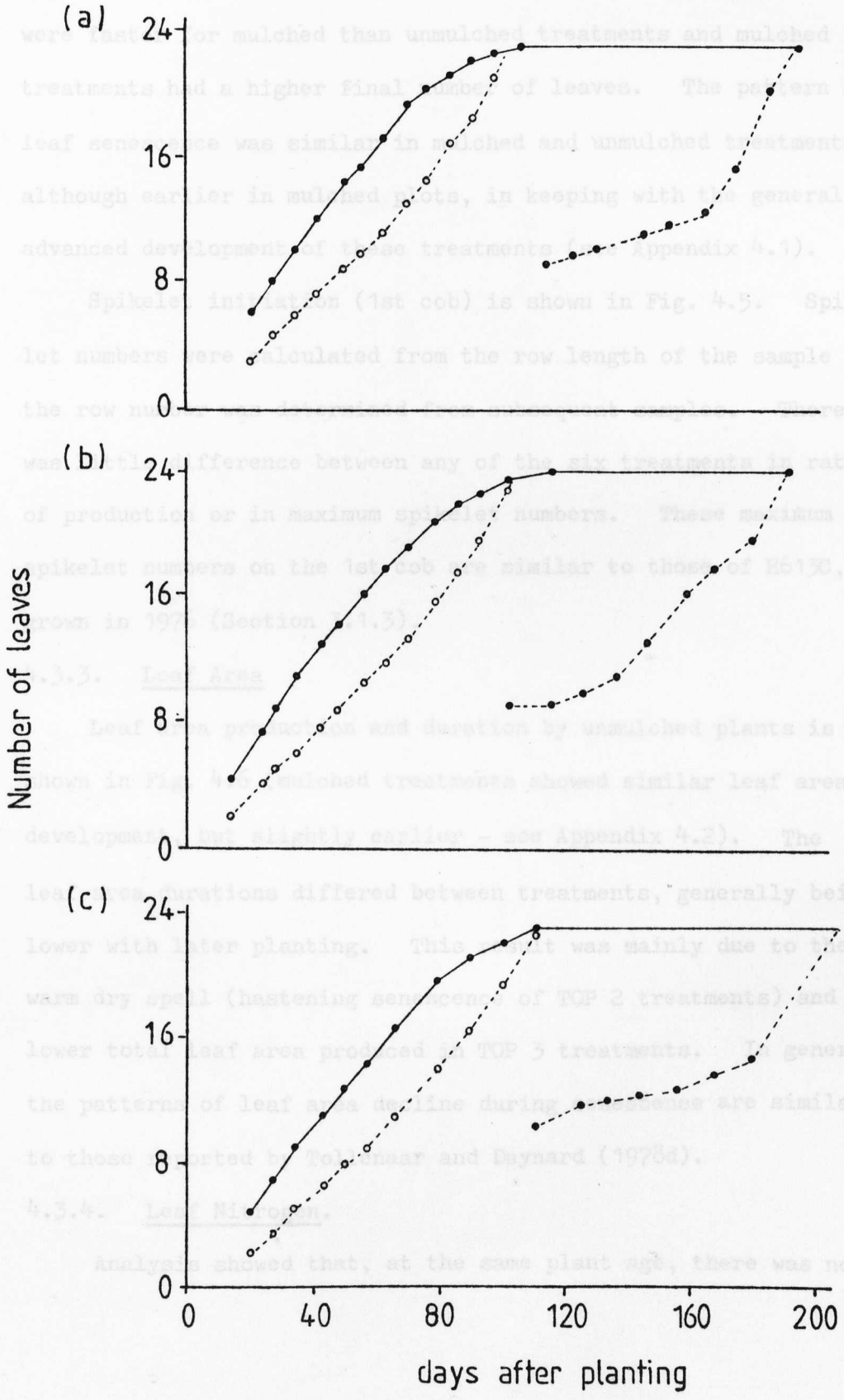
b) UM2

c) UM3

●——● appearance of leaf tip

o----o appearance of leaf collar

●·····● death of leaf


(a)
(b)
(c)
24
16
8
0
Number of leaves
0
40
80
120
160
200
days after planting

dry spell also occurred before this period. This finding agrees with a report by Claasen and Shaw (1970) that senescence may be hastened by moisture stress. Initial rates of leaf appearance were faster for mulched than unmulched treatments and mulched treatments had a higher final number of leaves. The pattern of leaf senescence was similar in mulched and unmulched treatments, although earlier in mulched plots, in keeping with the general advanced development of these treatments (see Appendix 4.1).

Spikelet initiation (1st cob) is shown in Fig. 4.5. Spikelet numbers were calculated from the row length of the sample and the row number was determined from subsequent samples. There was little difference between any of the six treatments in rates of production or in maximum spikelet numbers. These maximum spikelet numbers on the 1st cob are similar to those of H613C, grown in 1976 (Section 3.1.3).

4.3.3. Leaf Area

Leaf area production and duration by unmulched plants is shown in Fig. 4.6 (mulched treatments showed similar leaf area development, but slightly earlier - see Appendix 4.2). The leaf area durations differed between treatments, generally being lower with later planting. This result was mainly due to the warm dry spell (hastening senescence of TOP 2 treatments) and the lower total leaf area produced in TOP 3 treatments. In general, the patterns of leaf area decline during senescence are similar to those reported by Tollenaar and Daynard (1978d).

4.3.4. Leaf Nitrogen.

Analysis showed that, at the same plant age, there was no

Figure 4.5 Spikelet initiation and abortion.

a) M1 ● calculated spikelet number ■ counted spikelet number
UM1 ○ " " " □ " " "

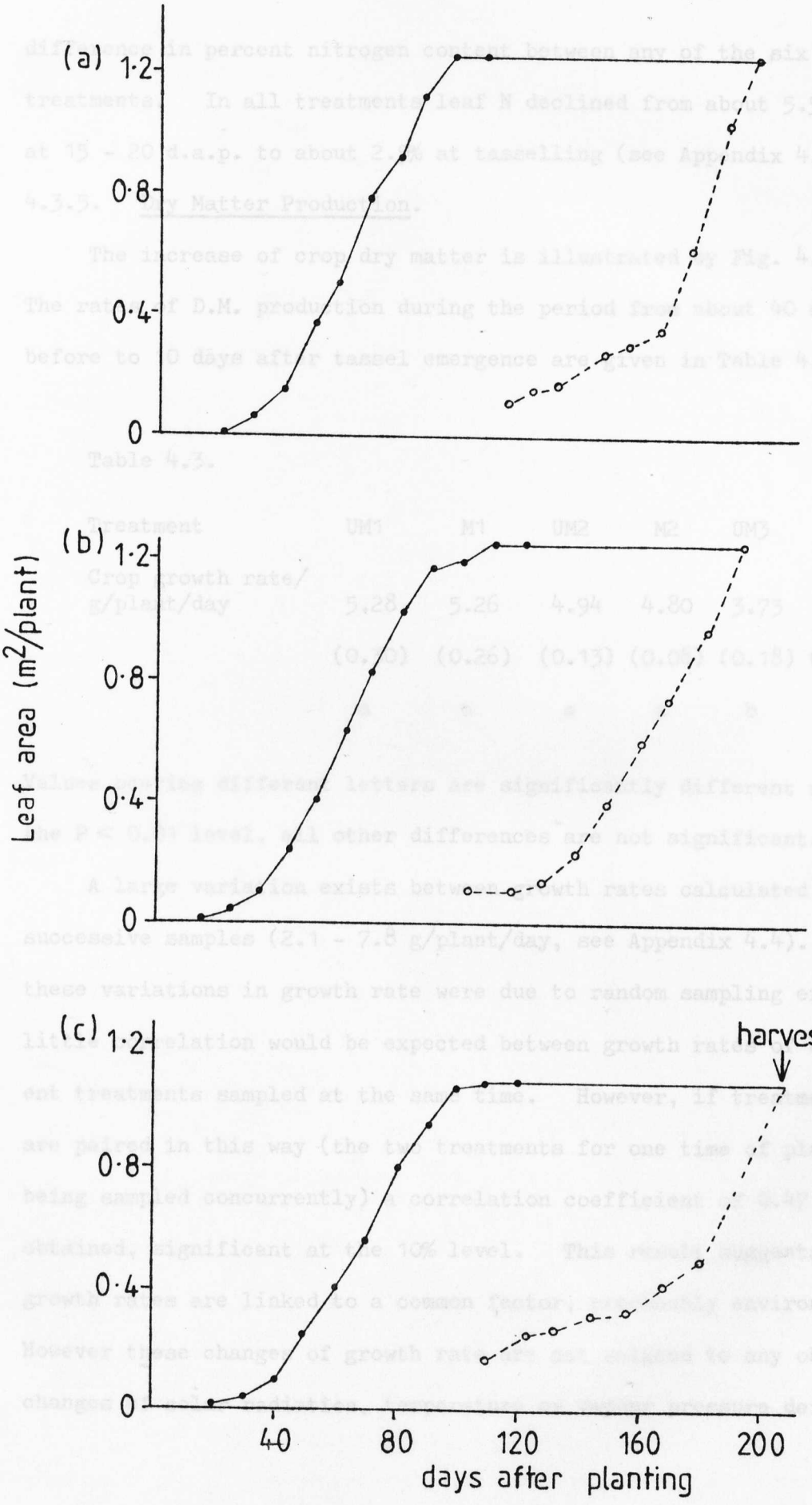
b) M2 ● " " " ■ " " "
UM2 ○ " " " □ " " "

c) M3 ● " " " ■ " " "
UM3 ○ " " " □ " " "

Figure 4.6 Leaf area.

		Calculated LAD (m^2day)
a)	UM1	129
b)	UM2	118
c)	UM3	104

- ● measured leaf area
- o calculated loss of green leaf area due to leaf death


(a)
1·2
0·8
0·4
0
(b)
1·2
0·8
0·4
0
Leaf area (m²/plant)
(c)
1·2
0·8
0·4
0
harvest
40
80
120
160
200
days after planting

difference in percent nitrogen content between any of the six treatments. In all treatments leaf N declined from about 5.5% at 15 - 20 d.a.p. to about 2.5% at tasselling (see Appendix 4.3).

4.3.5. Dry Matter Production.

The increase of crop dry matter is illustrated by Fig. 4.7. The rates of D.M. production during the period from about 40 days before to 10 days after tassel emergence are given in Table 4.3.

Table 4.3.

Treatment	UM1	M1	UM2	M2	UM3	M3
Crop growth rate/ g/plant/day	5.28	5.26	4.94	4.80	3.73	3.84
	(0.30)	(0.26)	(0.13)	(0.08)	(0.18)	(0.10)
	a	a	a	a	b	b

Values bearing different letters are significantly different at the $P < 0.01$ level, all other differences are not significant.

A large variation exists between growth rates calculated from successive samples (2.1 - 7.8 g/plant/day, see Appendix 4.4). If these variations in growth rate were due to random sampling error, little correlation would be expected between growth rates of different treatments sampled at the same time. However, if treatments are paired in this way (the two treatments for one time of planting being sampled concurrently) a correlation coefficient of 0.47 is obtained, significant at the 10% level. This result suggests that growth rates are linked to a common factor, presumably environmental. However these changes of growth rate are not related to any obvious changes of solar radiation, temperature or vapour pressure deficit.

Figure 4.7 Crop dry weight increase.

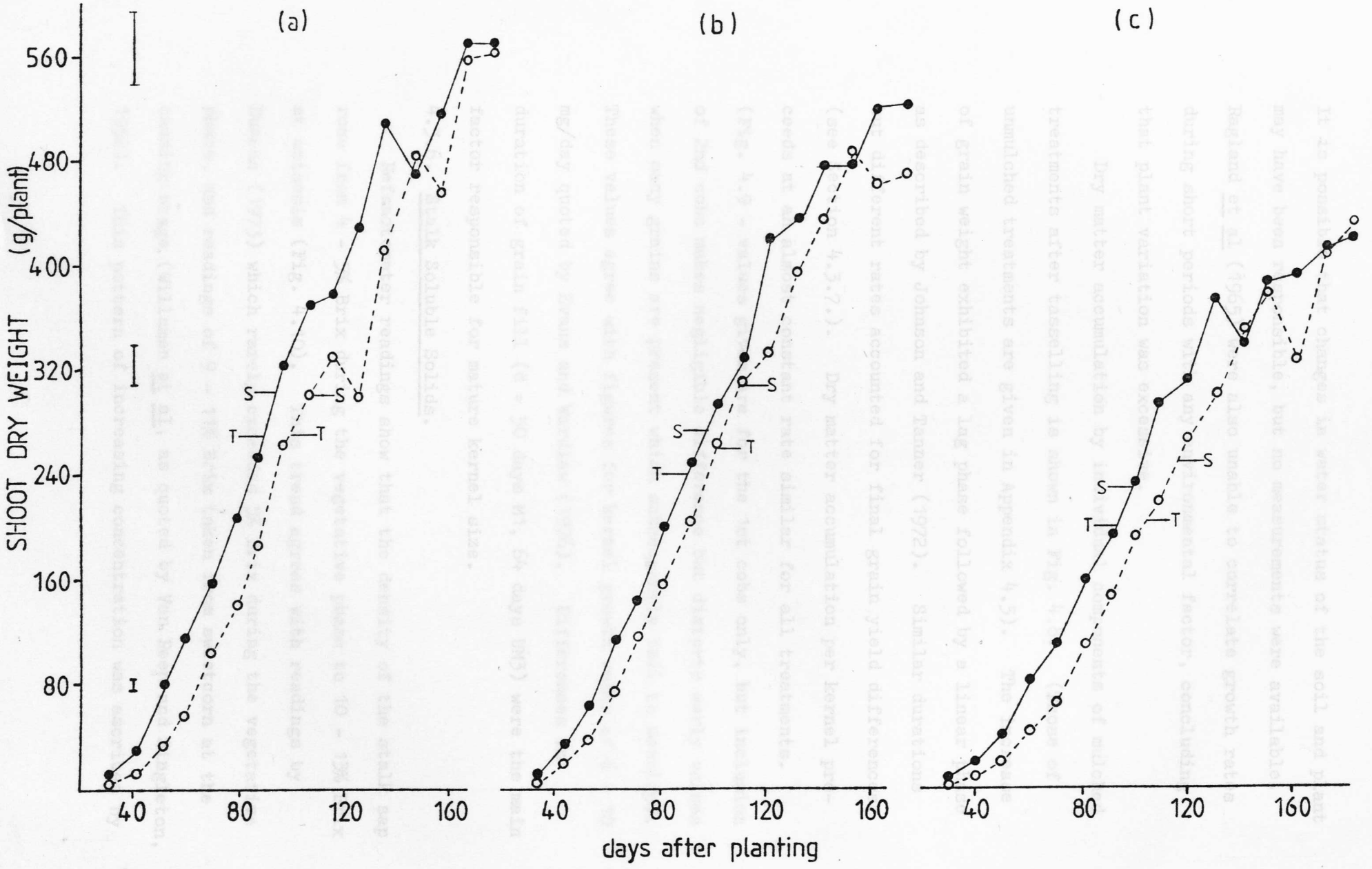
a) ● M1
   O UM1

b) ● M2
   O UM2

c) ● M3
   O UM3

S — - date of 50% silking

T — - date of 50% tassel emergence


(a)
(b)
(c)
SHOOT DRY WEIGHT (g/plant)
560
480
400
320
240
160
80
S
T
I
40
80
120
160
days after planting

It is possible that changes in water status of the soil and plant may have been responsible, but no measurements were available. Ragland et al (1965) were also unable to correlate growth rates during short periods with any environmental factor, concluding that plant variation was excessive.

Dry matter accumulation by individual components of mulched treatments after tasselling is shown in Fig. 4.8. (Those of unmulched treatments are given in Appendix 4.5). The increase of grain weight exhibited a lag phase followed by a linear phase as described by Johnson and Tanner (1972). Similar durations but different rates accounted for final grain yield differences (see Section 4.3.7.). Dry matter accumulation per kernel proceeds at an almost constant rate similar for all treatments. (Fig. 4.9 - values given are for the 1st cobs only, but inclusion of 2nd cobs makes negligible difference but distorts early values when many grains are present which subsequently fail to develop). These values agree with figures for kernel growth rates of 6 - 10 mg/day quoted by Evans and Wardlaw (1976). Differences in duration of grain fill (d = 50 days M1, 64 days UM3) were the main factor responsible for mature kernel size.

4.3.6. Stalk Soluble Solids.

Refractometer readings show that the density of the stalk sap rose from 4 - 5% Brix during the vegetative phase to 10 - 13% Brix at anthesis (Fig. 4.10). This trend agrees with readings by Duncan (1973) which rarely exceeded 5% Brix during the vegetative phase, and readings of 9 - 11% Brix taken from sweetcorn at the canning stage (Willamen et al, as quoted by Van Reen and Singleton, 1952). This pattern of increasing concentration was ascribed by

Figure 4.8 Weight changes of plant parts after flowering.

a) M1 b) M2 c) M3

○ stem dry weight

X leaf (blade and sheath) dry weight

□ husk and core dry weight

● grain dry weight

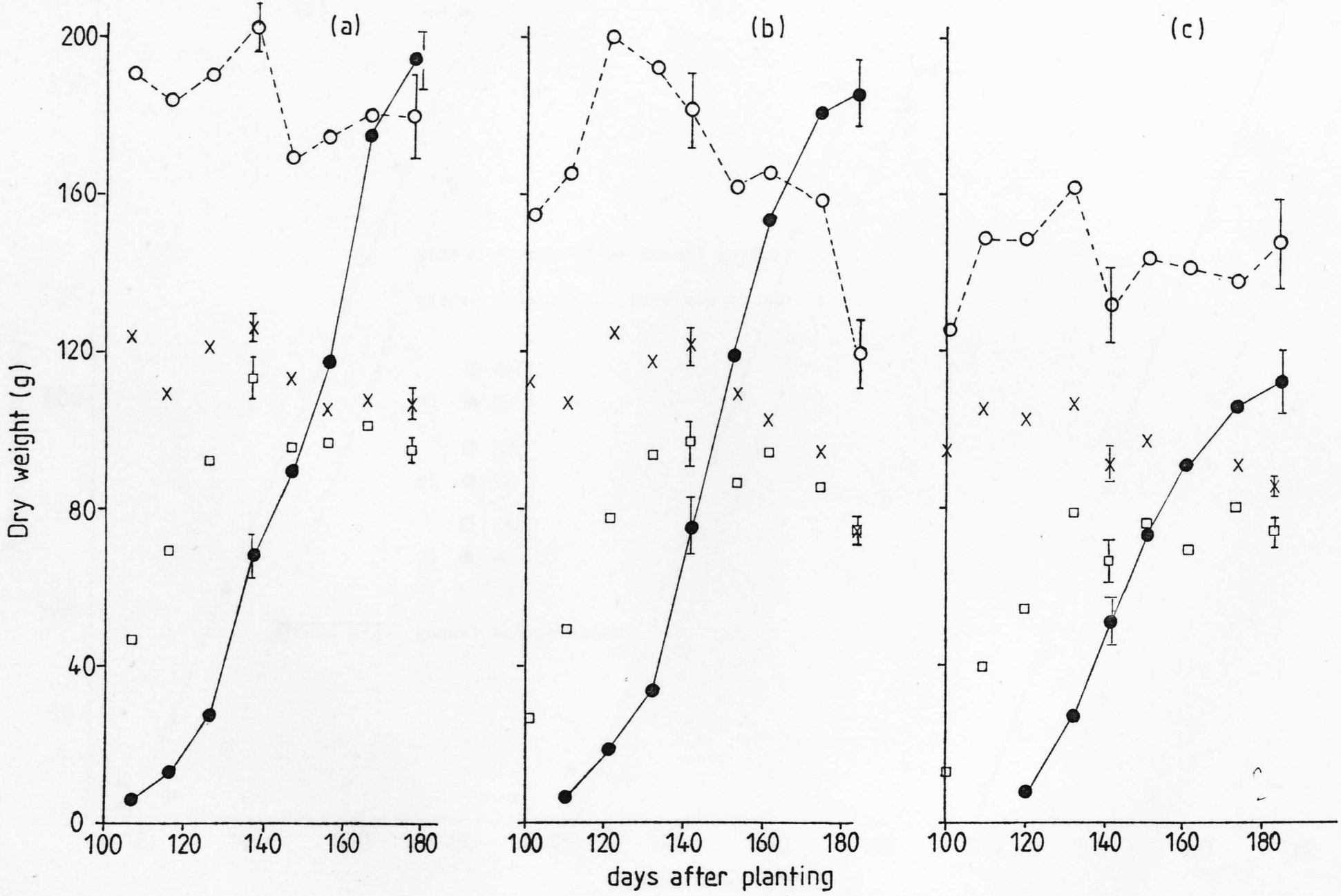

(a)
(b)
(c)
Dry weight (g)
0
40
80
120
160
200
100
120
140
160
180
days after planting

Figure 4.9 Kernel growth rate.

a) ● M1
   O UM1

b) ● M2
   O UM2

c) ● M3
   O UM3

Fitted regression lines are shown.

Arrows denote final kernel weight.

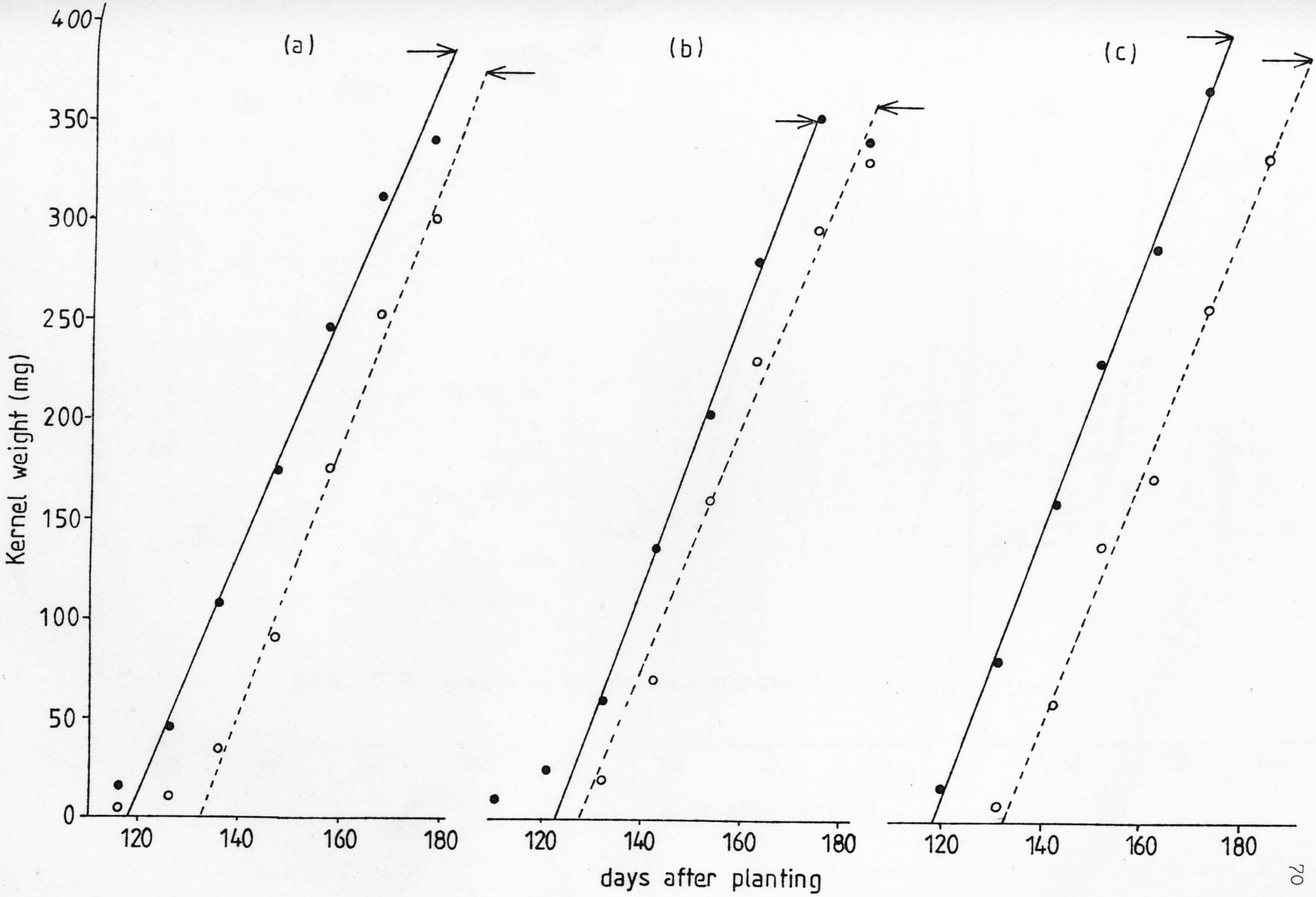

(a)
(b)
(c)
Kernel weight (mg)
0
50
100
150
200
250
300
350
400
120
140
160
180
days after planting

Figure 4.10 Changes of stalk density with time.

a) ● M1

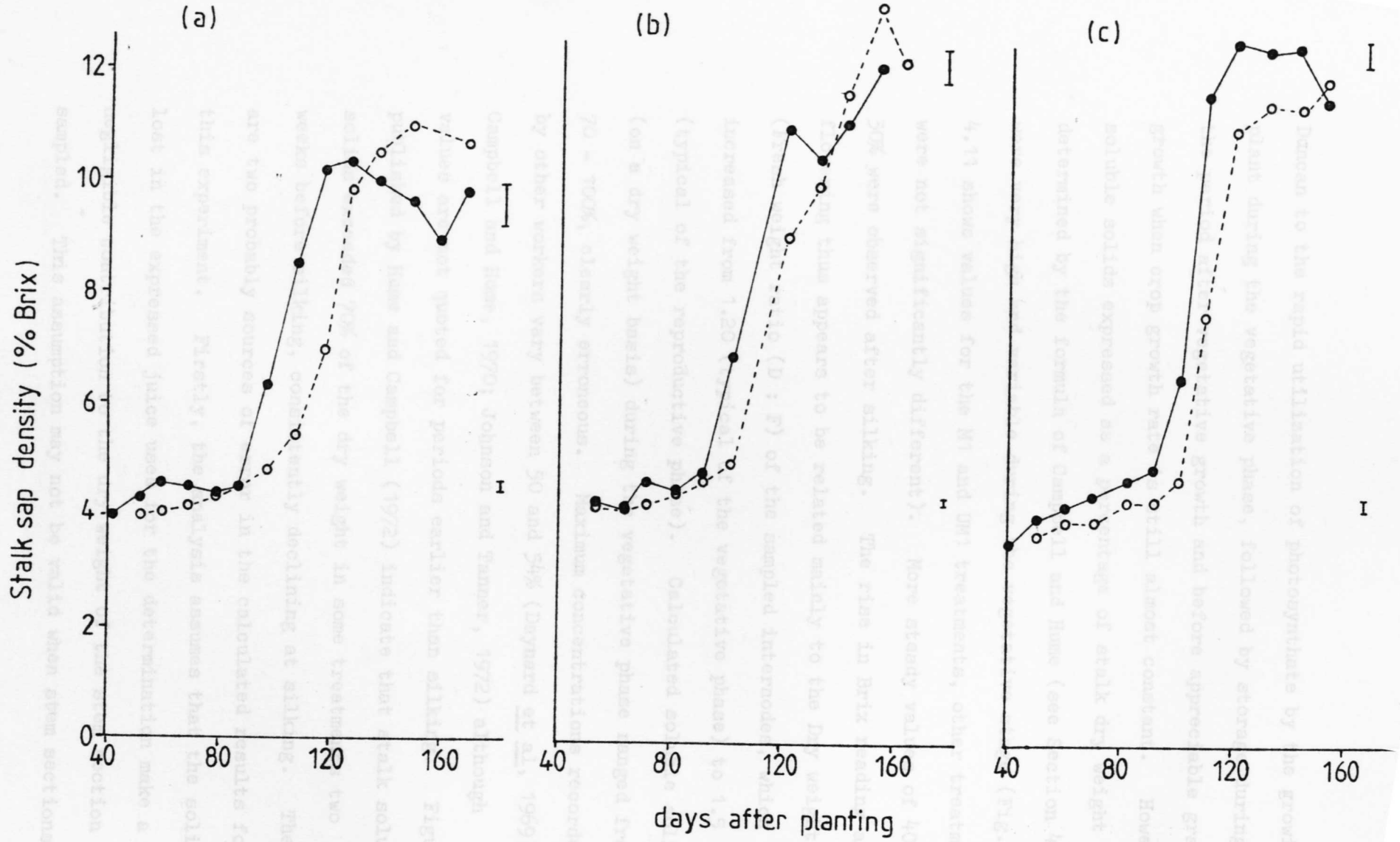
○ UM1

b) ● M2

○ UM2

c) ● M3

○ UM3


(a)
(b)
(c)
Stalk sap density (% Brix)
0
2
4
6
8
10
12
40
80
120
160
days after planting

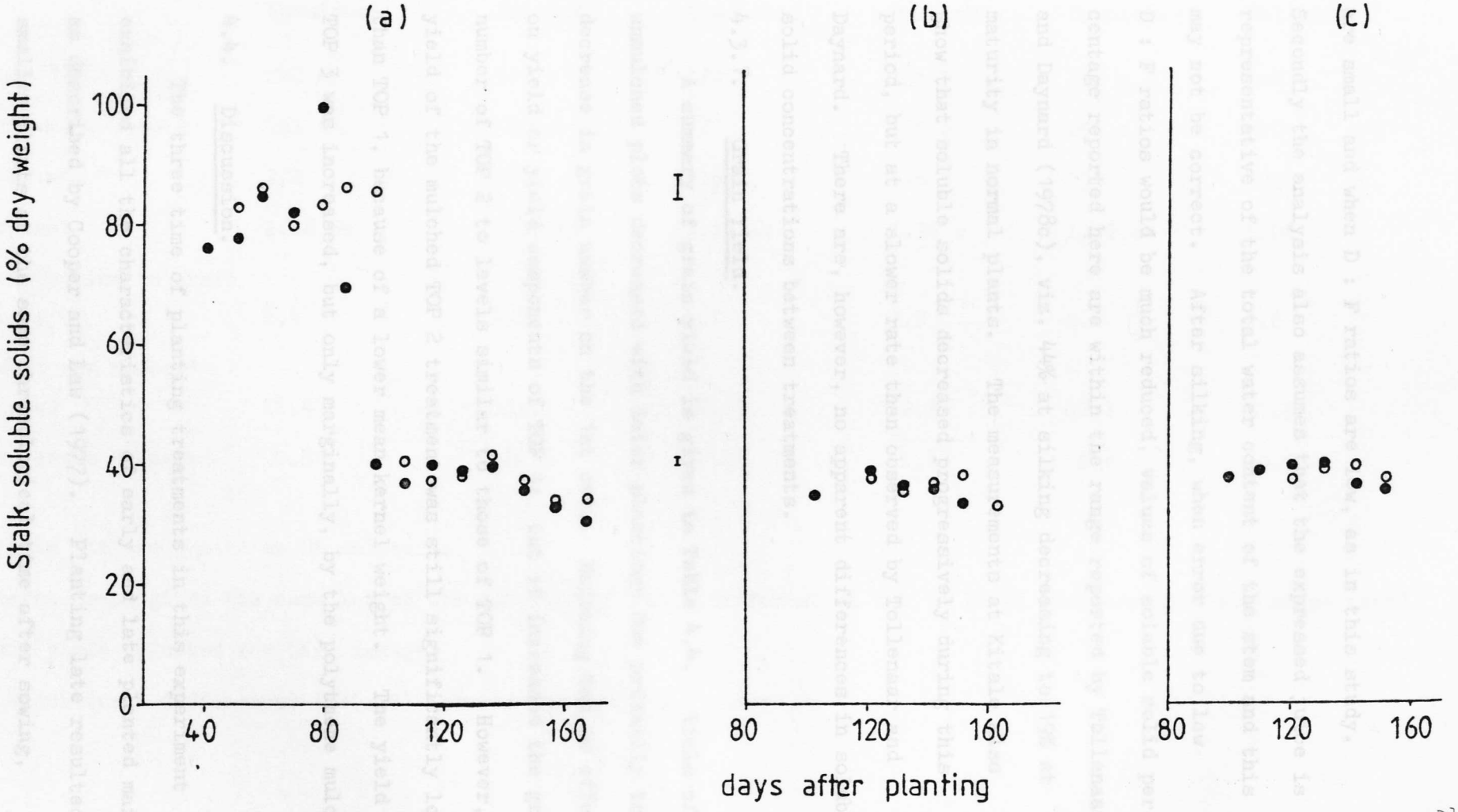
Duncan to the rapid utilization of photosynthate by the growing plant during the vegetative phase, followed by storage during the period after vegetative growth and before appreciable grain growth when crop growth rate is still almost constant. However, soluble solids expressed as a percentage of stalk dry weight determined by the formula of Campbell and Hume (see Section 4.2) were very high and variable during the vegetative stage (Fig. 4.11 shows values for the M1 and UM1 treatments, other treatments were not significantly different). More steady values of 40 - 30% were observed after silking. The rise in Brix reading at flowering thus appears to be related mainly to the Dry weight (Fresh weight ratio (D : F) of the sampled internodes, which increased from 1.20 (typical of the vegetative phase) to 1.5 (typical of the reproductive phase). Calculated soluble solids (on a dry weight basis) during the vegetative phase ranged from 70 - 100%, clearly erroneous. Maximum concentrations recorded by other workers vary between 50 and 54% (Daynard et al, 1969; Campbell and Hume, 1970; Johnson and Tanner, 1972) although values are not quoted for periods earlier than silking. Figures published by Hume and Campbell (1972) indicate that stalk soluble solids exceeded 70% of the dry weight in some treatments two weeks before silking, consistently declining at silking. There are two probably sources of error in the calculated results for this experiment. Firstly, the analysis assumes that the solids lost in the expressed juice used for the determination make a negligible contribution to the dry weight of the stem section sampled. This assumption may not be valid when stem sections

Figure 4.11 Stalk soluble solid percentage.

a) ● M1
   O UM1

b) ● M2
   O UM2

c) ● M3
   O UM3


(a)
(b)
(c)
Stalk soluble solids (% dry weight)
100
80
60
40
20
0
40
80
120
160
80
120
160
80
120
160
days after planting

are small and when D : F ratios are low, as in this study. Secondly the analysis also assumes that the expressed juice is representative of the total water content of the stem and this may not be correct. After silking, when error due to low D : F ratios would be much reduced, values of soluble solid percentage reported here are within the range reported by Tollenaar and Daynard (1978c), viz. 44% at silking decreasing to 19% at maturity in normal plants. The measurements at Kitale also show that soluble solids decreased progressively during this period, but at a slower rate than observed by Tollenaar and Daynard. There are, however, no apparent differences in soluble solid concentrations between treatments.

4.3.7. Grain Yield.

A summary of grain yield is given in Table 4.4. Yield of unmulched plots decreased with later plantings due primarily to the decrease in grain number on the 1st cob. Mulching had no effect on yield or yield components of TOP 1; but it increased the grain number of TOP 2 to levels similar to those of TOP 1. However, the yield of the mulched TOP 2 treatment was still significantly lower than TOP 1, because of a lower mean kernel weight. The yield of TOP 3 was increased, but only marginally, by the polythene mulch.

4.4. Discussion.

The three time of planting treatments in this experiment exhibited all the characteristics of early and late planted maize, as described by Cooper and Law (1977). Planting late resulted in smaller plants at the same chronological time after sowing,

Table 4.4. Grain Yield

	Top 1		Top 2		Top 3	
	Unmulched	Mulched	Unmulched	Mulched	Unmulched	Mulched
Grain Yield g/pl †	220 a	223 a	170 b	191 b	113 c	128 c
Grain number/plant †	593 c	580 c	473 b	550 c	290 a	320 a
1000 gr.wt. *	372	386	359	346	390	399
cobs/plant	1.18 bc	1.15 ab	1.16 ab	1.32 c	1.03 ab	1.02 a
% contribution to grain 2nd cob.	6.4	5.2	4.7	9.9	0.0	0.8
Spikelet row number* (1st cob)	12.4	12.6	12.2	12.3	12.1	11.9
% bird eaten kernels	0.8	0.5	0.0	1.1	2.4	0.9

All grain wts are quoted at 0% moisture.

Treatment means given the same letter are not significantly different at the 5% level (Duncans multiple range test)

† Grain yield adjusted for bird damage.

* No significant differences ($p<0.05$) between the treatment means

smaller plants at tasselling, smaller growth rates (during the linear phase of dry matter production) and smaller yields. Mulching TOP 1 and TOP 2 also had the expected effect: the growth and yield of early planted maize was largely unaffected, as soil temperatures are thought to be high enough to allow the genotypic potential to be fully expressed in the Kenya Highland environment, and the grain number of TOP 2 (mulched) was similar to that of TOP 1. Mulching of TOP 3, however, did not raise the yield or grain number significantly. This result does not agree with previous experiments at Kitale in 1974, 1975 and 1976 when polythene mulches raised the yields of late planted maize to levels typical of early planted maize. A possible reason for this discordant result is the period of drought experienced during late September and early October when TOP 3 treatments were flowering. Reductions in grain yield in excess of 40% following water stress at silking have been observed (Robins and Domingo, 1953; Denmead and Shaw, 1960; Barnes and Wooley. 1969; Claasen and Shaw, 1970). This dry spell could also have depressed the yield of the bare soil treatment. Further evidence that the yields of TOP 3 treatments may have been lowered by the drought is obtained by consideration of the mean soil temperatures of the bare soil plots during the early stages, which were only 0.7°C cooler for TOP 3 than TOP 1. (c.f. early and late planted soil temperatures of previous experiments - Table 4.1). It is unlikely that a 0.7°C lowering of soil temperature could cause a yield decrease of the magnitude observed in this experiment. If soil temperatures are the main cause of the time of planting effect.

The differences in yield in this experiment are rarely a result of differences in grain number. What differences there are in grain size are largely a consequence of duration of grain fill, which in turn can be explained by differences in air temperature during grain fill (see Table 4.5). That the final grain size is smaller at warmer temperatures (a finding supported by altitude trials - Cooper, 1979) is consistent with the apparant base temperature for the duration of grain filling being higher than the base temperature for the rate of filling (Table 4.5). An interesting corollary is that final kernel size is well correlated with the temperature during grain fill, but not with the length of the lag phase after flowering that precedes kernel filling. It therefore appears that kernel size is determined more by endosperm cell size than endosperm cell number, which is determined during the lag phase (c.f. studies of wheat by Brocklehurst, 1977). This finding contradicts a suggestion by Wilson and Allison (1978b) that grain size could be determined by the influence of temperature on the rate and duration of endosperm cell production, thus setting a maximum limit to kernel size soon after flowering.

As concluded from the previous year's experiment, grain number differences are more a consequence of the failure of grain to develop rather than the number initiated, and such failure may be a consequence of non-fertilization or subsequent abortion. Daynard and Duncan (1969) showed that fertilized but subsequently aborted grains exhibited a black layer in the placental region, but this type of observation did not prove reliable enough for

Table 4.5. Development and temperature after flowering.

Correlation	Correlation coefficient	significance[a]	base temperature °C
1/d(lag phase [b]) and mean air temperature.	0.79	*	10.8
1/d(lag phase) and mean air temperature omitting UM_2 treatment [c]	0.98	***	11.2
1/d(effective grain filling period) and mean air temperature	0.78	*	13.6
1/d(effective grain filling period) and mean temperature omitting UM2	0.93	**	14.4
rate of grain filling and mean air temperature	0.45	n.s	8.4
rate of grain filling and mean air temperature omitting UM2.	0.77	n.s	11.9
1/Wg(Where Wg is final grain size) and mean air temperature during effective filling period.	0.90	**	
1/Wg and mean air temperature during lag phase.	0.62	n.s.	

Notes. a *, **, *** denote significance at the 10%, 5% and 1% levels respectively

b Lag phase refers to the period from silking to zero grain weight (extrapolated from Fig 4.9)

c Fig. 4.9 shows a poor fitfor the UM2 treatment.

systematic determination of fertilization in this experiment. There is evidence that the synchronisation of tassel and silk emergence may be altered by time of planting (see Table 4.2), but more work is needed to determine whether the degree of non-fertilization is a major discriminant of yield at Kitale.

The results show a marked association between growth rate and final grain number ($r = 0.97$), agreeing well with previous (and very diverse) experiments at Kitale (Fig. 4.12). If the growth rate is expressed on a thermal time basis, then the results from other sites, at different temperatures, also show this association (Fig. 4.12). This relationship suggests that grain viability and hence yield is determined by the interaction between crop growth rate and development rate. Such a relationship could either be mediated by direct competition for assimilates or by a more indirect mechanism, involving hormone levels for example. These findings add to the speculations of others concerning assimilate supply and kernel abortion (see Section 2.2.1.) and highlight the need for a better understanding of such interactions.

Further consideration of the results of this experiment shows that growth rate of the M3 treatment, determined <u>before</u> the dry spell, was not much improved by the mulch, and yet it was suggested above that the yield of this treatment was limited by the dry spell. This result can be explained in two ways:

either a) mulching the late planted maize in this experiment would not have improved yield even if the drought had not occurred,

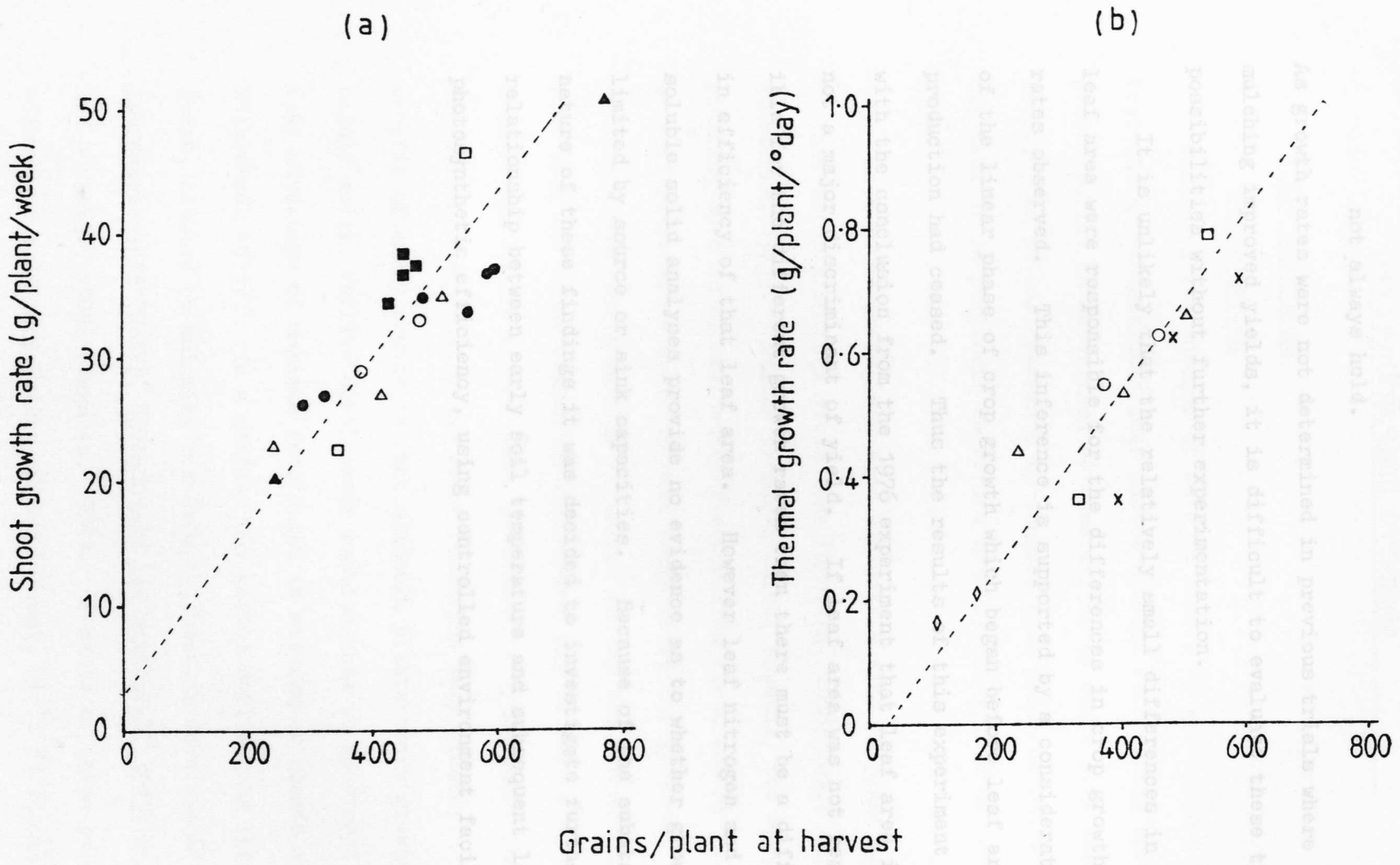
Figure 4.12 The relation between growth rate and grain number.

a) Growth rate expressed in calendar time (all crops grown at Kitale).
r = 0·93

b) Growth rate expressed in thermal time.
r = 0·89

■ -1976 Mulch and seed size experiment.
▲ -1976 Plant population experiment.
● -1977 Time of planting and mulch experiment.
) See Chapter 3

△ -1976 Time of planting experiment (Kitale).
□-1975 Weed experiment (Kitale).
○ -1976 Growth regulator experiment (Kitale).
x -1977 Altitude experiment.
◊ -1977 Mulch experiment (Mombasa).
) data from Cooper, 1979


(a)
(b)
Shoot growth rate (g/plant/week)
Thermal growth rate (g/plant/°day)
Grains/plant at harvest
0
10
20
30
40
50
0·2
0·4
0·6
0·8
1·0
200
400
600
800

or b) the relationship between growth rate and yield does not always hold.

As growth rates were not determined in previous trials where mulching improved yields, it is difficult to evaluate these two possibilities without further experimentation.

It is unlikely that the relatively small differences in leaf area were responsible for the differences in crop growth rates observed. This inference is supported by a consideration of the linear phase of crop growth which began before leaf area production had ceased. Thus the results of this experiment agree with the conclusion from the 1976 experiment that leaf area is not a major discriminant of yield. If leaf area was not responsible for the different growth rates then there must be a difference in efficiency of that leaf area. However leaf nitrogen and stem soluble solid analyses provide no evidence as to whether growth is limited by source or sink capacities. Because of the substantial nature of these findings it was decided to investigate further the relationship between early soil temperature and subsequent leaf photosynthetic efficiency, using controlled environment facilities.

5. TEMPERATE FIELD STUDIES, SOIL TEMPERATURE AND PHOTOSYNTHETIC EFFICIENCY

5.1 Field experiment

5.1.1. Introduction

Following the outcome of work in Kenya, it was decided to test the hypothesis that leaf photosynthesis rate during the main growth period is determined to some extent by early soil temperature. As it was necessary to conduct this phase of the work in England, it is pertinent to review briefly the growth of temperate maize.

Maize grown in England also exhibits a time of planting effect, in that later plantings yield less (Bunting, 1968; Osafo and Milbourne, 1975). Unlike tropical maize, however, the earliest planting date is determined by freedom from frost and by the rise of soil temperature above to base temperature for growth. Later plantings have the advantage of warmer soils, but run an increased risk that the final stages of development may be halted by cold weather and frosts at the onset of winter. Throughout the growing season, temperature and solar radiation vary greatly. The benefit of early sowing is that although plants start growing in colder soils, earlier development enables them to intercept and take advantage of maximum insolation in mid-summer (Osafo and Milbourne, 1975). In a similar way warmer soil during the early phase, induced by mulching for example, hastens development and increases yield (Watts, 1970; Osafo and Milbourne, 1975; Phipps and Cochrane, 1975; Liakatas, 1978). Because of these overriding effects of soil temperature on development, it is difficult to

establish from published work whether warm soils are beneficial for other reasons, as suggested by the Kenyan work.

In the absence of firm information about the effect of soil temperature on temperate maize, other than on timing of development, it was decided to impose different soil temperatures in the field, in such a way that different treatments would flower at approximately the same time.

It has already been noted that the period during which warmer soils effectively raise maize yields in Kenya corresponds to the period during which the apical meristem is below ground level (Cooper and Law, 1978a). There is no other evidence, however, that the meristem perceives temperature and is primarily responsible for the processes that eventually lead to higher yields. Furthermore although soil heating is one of the prime effects of polythene mulches, mulches do have other consequences and other methods of soil heating have not been used on tropical maize. It was therefore decided to compare the effects of soil heating by mulching with more direct heating of the shoot meristematic region, using heating coils.

The main objectives of this phase of the project were thus:

1) To determine whether warm soils conferred yield advantage in English conditions, other than by hastening plant development;

2) To determine whether the meristem is the site of perception for such a response provided its existence can be demonstrated;

3) To determine whether photosynthetic efficiency during the main growth period was related to early soil temperatures.

5.1.2. Materials and Methods.

The experimental area (located at field 12, Sutton Bonington) was cultivated in April 1978 and a heavy dressing of complete fertilizer was applied. The experimental design consisted of three randomised blocks of the following three treatments:

P - Polythene mulch.

H - Heating coils.

B - Bare soil control.

Each plot consisted of five rows, 0.5 m apart, containing three sample rows. Each row consisted of 24 plants, spaced 22.5 cm apart. This high plant density, 89,000 plants/ha was chosen to hasten the time of full crop cover and to enable two samples to be taken to determine crop growth.

The B treatment was sown with Zea mays (var. Kelvedon Glory) on 23 May, 1978, at 5 cm depth, after a previous sowing (9 May) was killed by the frost. The H treatment was sown on 5 June, seeds being sown between two Autogrow 500 W heating cables buried at approximately 2 cm depth and 2 cm apart. For the P treatment planted on 6 June, the mulch was applied as described in Chapter 3. Soil temperatures at 3 cm and 7 cm depth, and air temperatures were monitored by Grant recorder. Soil heating in the P and H treatments was discontinued on 20 and 21 July, when development of all treatments was approximately synchronous.

Photosynthesis rates were measured between 1 August 1978 and 10 August 1978 using the mobile IRGA system described by Marshall and Biscoe (1977). During this period conditions were generally overcast, and plants were well watered the day before measurements

were taken. Measurements were taken on the 9th leaf, when this or the 10th leaf was the youngest fully expanded leaf. As natural irradiance was low and variable, the leaves were illuminated with a 400 W sodium vapour lamp. Photosynthetically active radiation (PAR) was measured with a Lambda quantum sensor. A water trough (4 cm deep) above the perspex leaf chamber (area 21 cm^2), and water circulating within the walls of the chamber (1 cm depth) reduced the heating effect of the lamp. Changes in the temperature of the water circulating within the chamber walls modified leaf temperature only slightly - 40°C change in wall temperature caused an 8°C change in leaf temperature. Once the leaf had been placed in position, leaf photosynthesis and transpiration were allowed to equilibrate for about 30 min. Stepwise reductions in irradiance were then obtained by a series of neutral filters, and the photosynthesis rate was measured when it became steady, usually within 1 min. Transpiration rates equilibrated more slowly. Leaf temperatures, measured using thermistor probes, decreased by about 3°C during this period, and starting temperature varied between 20 - 23°C for different leaves. Hourly ambient CO_2 levels were obtained from a seperate departmental record and hourly ambient vapour pressure was measured using an Assmann psychrometer.

Using the IRGA to measure evaporation from wet blotting paper the boundary layer resistance to water vapour transfer in the leaf chamber, r_a, was found to be 0.35 scm^{-1}. This was converted to a boundary layer resistance to carbon dioxide transfer, r_a', of 0.48 scm^{-1} by the method of Jarvis (1971).

5.1.3. Results

Severe cold weather in the period following sowing, caused death of the main stem of most seedlings of the B treatment and some of the H treatment. The P treatment was unaffected. Tillers subsequently developed on these damaged plants, one tiller usually becoming dominant and eventually bearing normal cobs. Due to this cold damage it was impossible to determine crop growth rate. Leaf appearance and subsequent measurements were taken from plants judged to be unaffected by the cold spell. Leaf area and initiated spikelet number were determined from a sample of 20 plants and final harvest from a further sample of 30.

5.1.3.1. Temperature and development.

Both the mulch and the heating coils raised the soil temperature at 3 cm depth by about 4°C. The temperature increase at 7 cm depth under polythene was similar but was only about 2°C under the heating coils. That both treatments were equally effective in heating the meristem was shown by similar rates of leaf appearance, the 11th leaf being reached at 43 and 42 d.a.p. in the P and H treatments respectively. The B treatment reached the 11th leaf stage 54 d.a.p. The corresponding dates of the 11th leaf stage were 16, 17 and 19 July in the B, H and P treatments, and thereafter development of the crop was approximately synchronised, depending primarily on air temperature. A regression of leaf appearance on mean weekly temperatures (using soil before the 11th leaf stage, and air temperatures thereafter) gave a coefficient of 0.81 and a base temperature of 8.7°C. This figure is consistent with base temperatures obtained in Kenya and in previous work at Sutton Bonington (Watts, 1970; Liakatas, 1978).

5.1.3.2. Leaf area development.

Individual leaf areas are shown in Fig. 5.1. The B and H treatments showed a similar pattern of leaf size but out of phase due to a greater number of leaves initiated by the H treatment. Thus the total leaf area produced by the two treatments was similar - 2,120 and 2,140 cm^2 respectively. In the P treatment however, leaves were larger and formed a total area of 2,700 cm^2. As leaf expansion is highly sensitive to water stress, this result indicates that the moisture conserving properties were also an important feature of the mulch (even though all plots were watered when tensiometers indicated a soil water deficit above 0.25 bar at 7 cm depth). This leaf area increase could be significant for dry matter production in this experiment as the total leaf area index produced by the P treatment was only 2.4, probably not sufficient to intercept all the available radiation. These low values of L.A.I., even at the high plant density used, indicate the poor nature of the 1978 summer for maize growth.

5.1.3.3. Spikelet and grain numbers.

Maximum and surviving spikelet numbers are recorded in Table 5.1. There appeared to be slight differences in number of spikelets produced on the first and second cobs, due mainly to row number, rather than row length. However, these differences are not significant. Final grain numbers showed that less than half of the potential grain sites on the 1st cob were realised and there was little difference in number filled between treatments. Final grain size was impossible to determine because the onset of colder weather stopped development.

Figure 5.1 Individual leaf area of field grown maize.

● mulched plants

□ cable heated plants

○ unheated plants

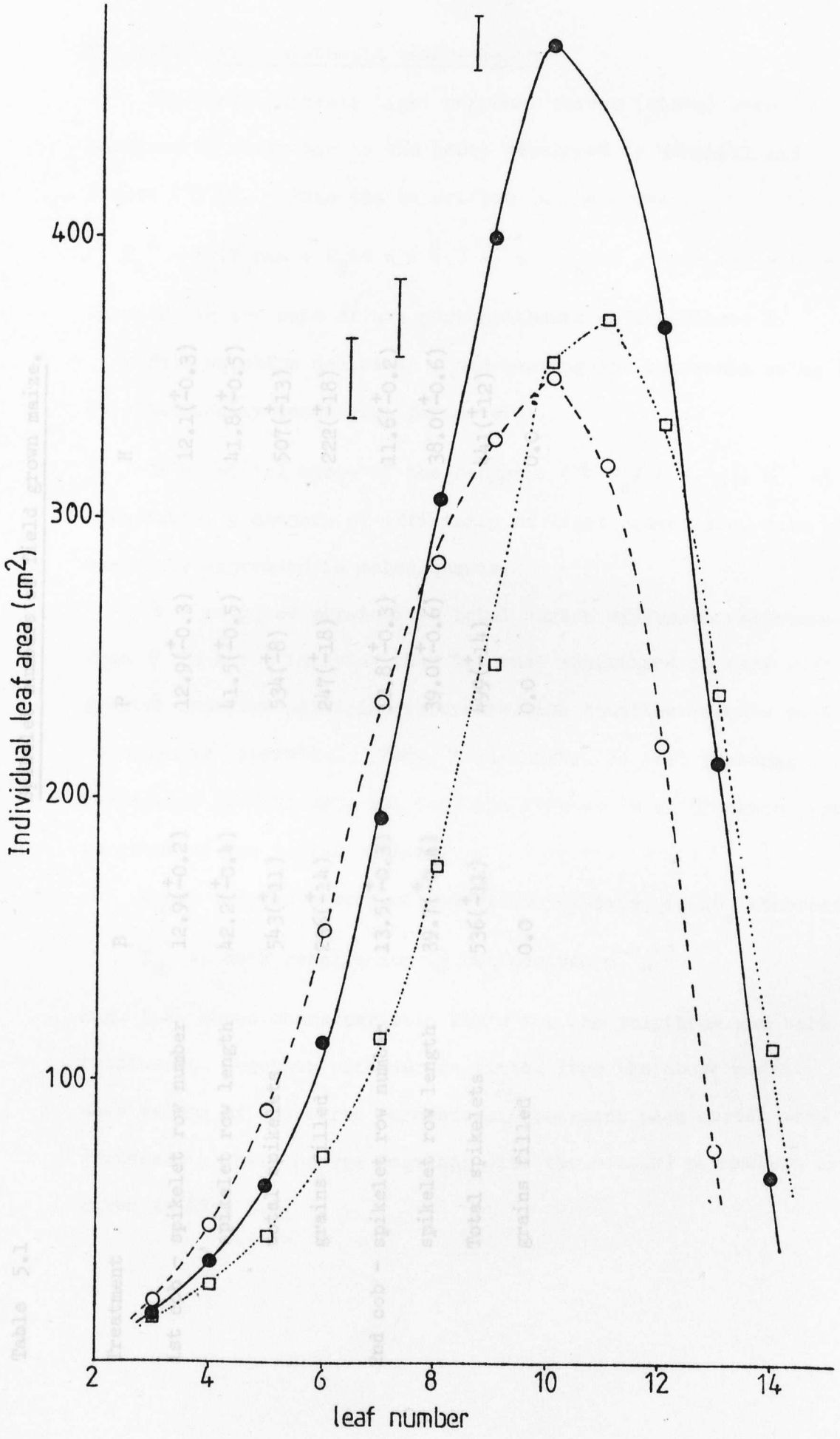

Individual leaf area (cm2)
400
300
200
100
2
4
6
8
10
12
14
leaf number

Table 5.1 Spikelet numbers of field grown maize.

Treatment	B	P	H
1st cob - spikelet row number	12.9($\pm$0.2)	12.9($\pm$0.3)	12.1($\pm$0.3)
spikelet row length	42.2($\pm$0.4)	41.5($\pm$0.5)	41.8($\pm$0.5)
total spikelets	543($\pm$11)	534($\pm$8)	507($\pm$13)
grains filled	236($\pm$14)	247($\pm$18)	222($\pm$18)
2nd cob - spikelet row number	13.5($\pm$0.3)	12.8($\pm$0.3)	11.6($\pm$0.2)
spikelet row length	39.7($\pm$0.6)	39.0($\pm$0.6)	38.0($\pm$0.6)
Total spikelets	536($\pm$11)	499($\pm$14)	441($\pm$12)
grains filled	0.0	0.0	0.0

5.1.3.4. Photosynthesis measurements.

The photosynthesis light response curves (PLR's) were analysed by reference to the model developed by Marshall and Biscoe (1979). This can be written in the form:

$$\theta P_n^2 - P_n(P_n max + R_d(1 - 2\theta) + \alpha I P_n max - R_d(P_n max + (1 - \theta)R_d) = 0$$

where P_n is the rate of net photosynthesis at irradiance I.

This equation describes a non-rectangular hyperbola using four physiologically meaningful parameters:

α = initial slope of the response ($\delta P_n / \delta I$, $g \mu E^{-1}$ at zero irradiance, a measure of efficiency of light conversion, more conveniently expressed in moles/quanta.

θ = ratio of physical to total carbon diffusion resistance. When θ is zero, implying that internal resistance is very much greater than the physical resistance, the equation reduces to a rectangular hyperbola. When θ is unity, so that physical resistance is dominant, the equation reduces to a 'Blackman type' response of two linear phases.

$P_n max$ = maximum rate of net photosynthesis, (g CO_2 absorbed $m^{-2}h^{-1}$)

R_d = dark respiration (g CO_2 evolved $m^{-2}h^{-1}$)

Fig. 5.2. shows characteristic PLR's for the polythene and bare soil treatments, together with curves fitted from the above model. From mean values of the curve parameters, treatment mean curves were constructed. These curves together with the related parameters are given in Fig. 5.3.

Figure 5.2 Characteristic net photosynthesis-light response curves for the mulched (●—●) and unheated (O--O) plots. (9th leaf).

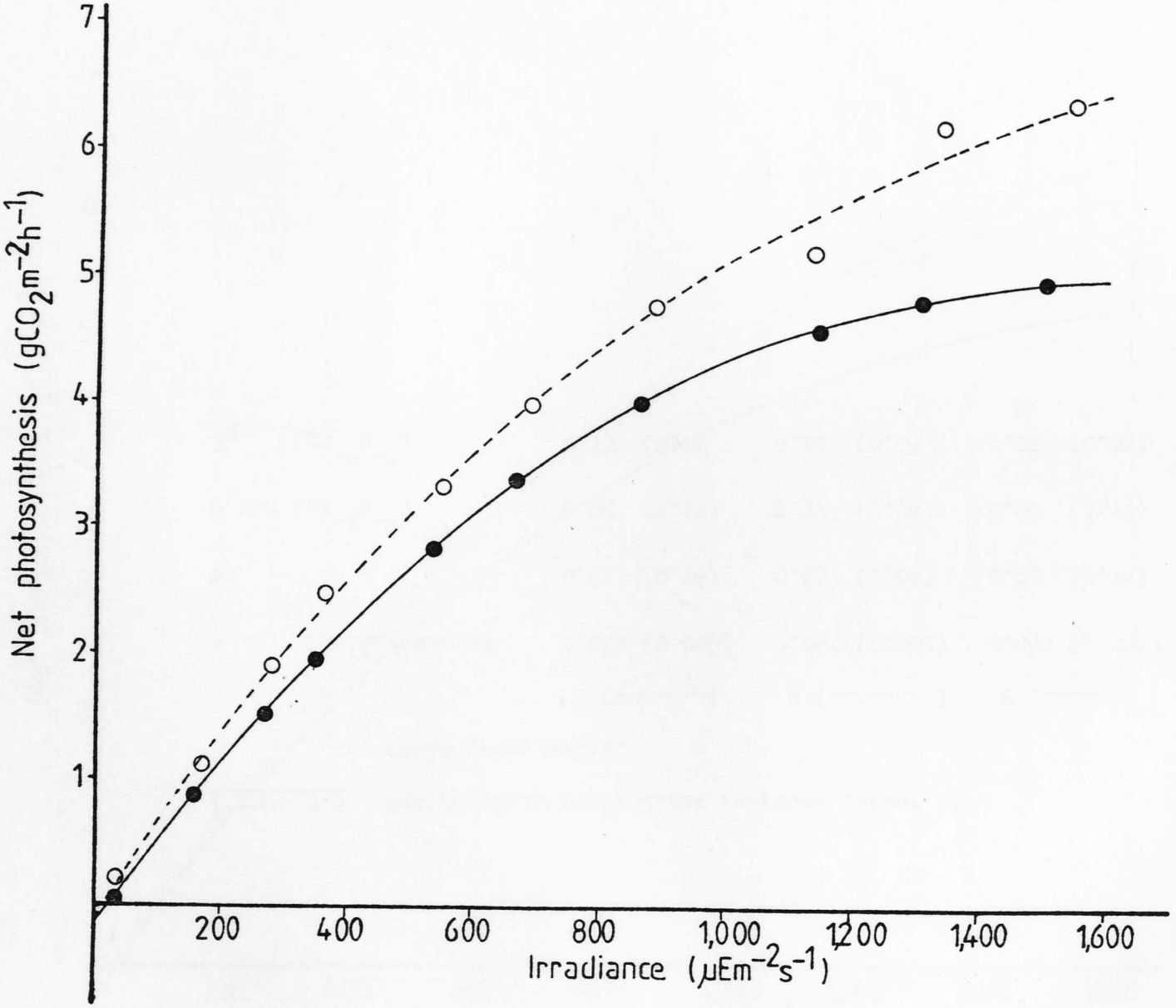
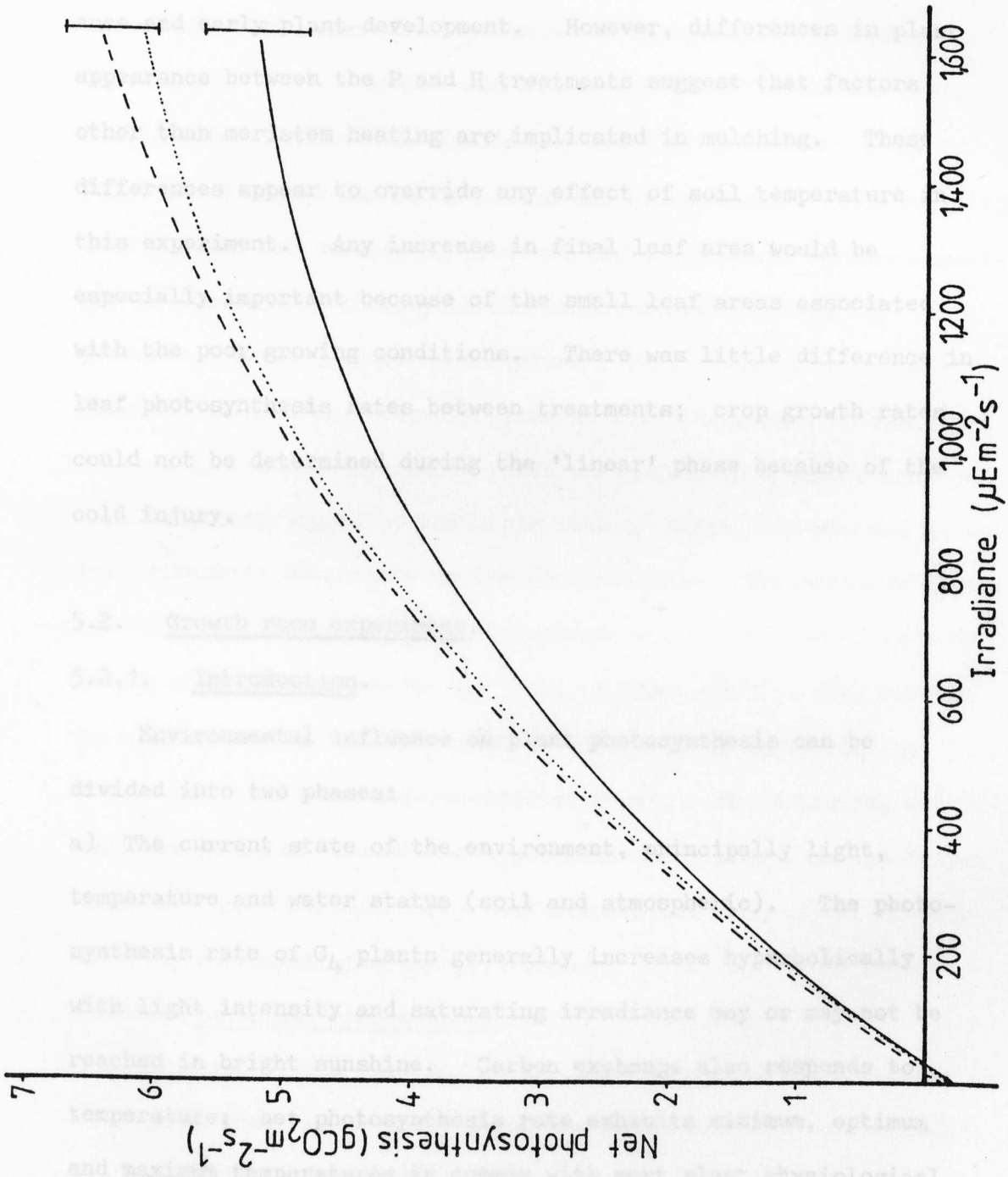

Net photosynthesis ($gCO_2m^{-2}h^{-1}$)
7
6
5
4
3
2
1
200
400
600
800
1,000
1,200
1,400
1,600
Irradiance ($\mu Em^{-2}s^{-1}$)

Figure 5.3 Net photosynthesis-light response curves of field grown maize.

		B (- - - - -)	H (.....)	P (———)
α	(moles/quanta)	0.047 (0.004)	0.043 (0.002)	0.041 (0.003)
θ		0.61 (0.16)	0.83 (0.04)	0.75 (0.11)
$P_n max$	($gm^{-2}h^{-1}$)	9.58 (1.11)	7.57 (0.74)	6.64 (1.17)
R_d	($gm^{-2}h^{-1}$)	0.13 (0.07	0.22 (0.06	0.09 (0.03)


Net photosynthesis ($gCO_2 m^{-2} s^{-1}$)
1
2
3
4
5
6
7
200
400
600
800
1,000
1200
1400
1600
Irradiance ($\mu E m^{-2} s^{-1}$)

5.1.4. Discussion and conclusions.

Poor weather made the aims of this experiment difficult to achieve. That the heating coils were as effective as the mulch in warming the meristem is evident from the rates of leaf appearance and early plant development. However, differences in plant appearance between the P and H treatments suggest that factors other than meristem heating are implicated in mulching. These differences appear to override any effect of soil temperature in this experiment. Any increase in final leaf area would be especially important because of the small leaf areas associated with the poor growing conditions. There was little difference in leaf photosynthesis rates between treatments; crop growth rates could not be determined during the 'linear' phase because of the cold injury.

5.2. Growth room experiment.

5.2.1. Introduction.

Environmental influence on plant photosynthesis can be divided into two phases:

a) The current state of the environment, principally light, temperature and water status (soil and atmospheric). The photosynthesis rate of C_4 plants generally increases hyperbolically with light intensity and saturating irradiance may or may not be reached in bright sunshine. Carbon exchange also responds to temperature; net photosynthesis rate exhibits minimum, optimum and maximum temperatures in common with most plant physiological processes. Dry air may cause stomata to close thereby regulating photosynthesis, as may adverse plant water status.

b) The previous state of the environment. Many workers have shown that the photosynthetic rate of leaves depends on their thermal history (Hesketh, 1968; Treharne and Eagles, 1970; Ludlow and Wilson, 1971; Bird et al, 1978). Light levels during growth are also important (Bjorkman and Holmgren, 1963; Ludlow and Wilson, 1971). Ludlow and Wilson (1971) and Doley and Yates (1976) found that acclimatization by tropical grasses to a new temperature regime can occur within one or two days. This suggests that temperature during the previous day or so would be more important in determining photosynthesis than temperatures during previous growth. Fussel and Pearson (1978) however, have shown that millet plants previously grown at lower temperatures exhibited relatively low photosynthesis rates when moved to a warmer environment, and they suggested that this lack of adaptation was due to the leaf structure determined during pretreatment. The question of how much of the effect of growth temperature can be attributed to temperatures within the previous day or so, and how much is attributable to earlier more permanent change is difficult to answer in the absence of consistent experimental evidence. The following experiment was designed to test the hypothesis formulated from the Kenyan phase of this work that early soil temperatures can affect subsequent crop photosynthesis and performance.

5.2.2. Materials and Methods.

Zea mays (Kenya var. H6302) was sown into John Innes compost in 5" pots that had previously had the basal drainage holes sealed. The pots were immersed in three separate water baths maintained at 15°C, 20°C and 25°C, hereafter designated cold, medium and hot treatments respectively. A 1 cm layer of perlite was applied to

the surface of the compost. Water status was maintained by filamentous wicks, supplemented by hand watering during the later stages when the wicks alone were not adequate. Day (13 hr.)/ Night (11 hr.) room temperature was maintained at 22/15°C; close to the mean day/night temperatures at Kitale. Light was supplied from a mixture of mercury and sodium lamps giving about 300 μ $Em^{-2}s^{-1}$ photosynthetically achieve radiation at pot level. Plants were removed from the water baths and transplanted into 12" pots at the 10th visible leaf stage.

Photosynthesis measurements were taken on the 10th leaf, when fully expanded, using the IRGA system described by Marshall and Biscoe (1977). Five plants were measured from the hot and cold treatments and four from the medium treatment. Individual plants were transferred to a second growth room 40 minutes before the leaf chamber was attached, and replaced immediately after measurements had been taken. This second growth room containing the leaf chamber, was preset to 23, 30, 16, 8, 40 and 23°C over six successive days to obtain measurements over a range of temperatures. Leaf temperature (within the leaf chamber) equilibrated within 4°C of the room temperature. The remainder of the IRGA, except for that part of the recirculating loop containing the leaf chamber, was situated outside the growth room. After photosynthetic measurements had been completed, the 10th leaf was analysed for nitrogen.

Water vapour concentrations of the IRGA air intake were measured hourly, and CO_2 concentration was assumed to be 330 ppm except for calibration when spot readings were taken. Where room temperatures were below the dew point of incoming air, the air was dried through

magnesium perchlorate. Leaf photosynthesis and transpiration rates were allowed to equilibrate for about 30 min. and then irradiance (from a Sodium vapour lamp) was reduced stepwise through a series of neutral filters, CO_2 evolution being allowed to equilibrate at each step.

5.2.3. Results

5.2.3.1. Characterisation of growth environment.

Isothermal soil conditions are difficult to obtain within pots placed in a growth room, due to the heating effect of the light. In this experiment air temperatures, different from pot temperatures, also exerted an influence on soil temperature. The only effective method of dispensing with this problem is to use completely submerged containers (Walker, 1969). The modification of soil temperature within the pots in this experiment is illustrated by Fig. 5.4. Dissection of thinned plants (at the 5th leaf stage) showed that the apical meristem was about 1.5 cm below soil level, and reference to Fig. 5.4. gives mean soil temperatures at 2 cm depth of 23°C, 20°C and 17°C in the hot, medium and cold treatments respectively.

5.2.3.2. Photosynthesis measurements.

The data were analysed as described in Section 5.1.3.4: characteristic PLR curves of the hot treatment, measured at various leaf temperatures, are given in Fig. 5.5. The response of net photosynthesis to light was similar to other published work (e.g. Hesketh and Musgrave, 1962). Saturating irradiances were generally not reached, the exception being one or two plants at low

Figure 5.4 Soil temperature deviations from water-bath temperature (Representative profiles from each treatment at the end of a day and a night period.)

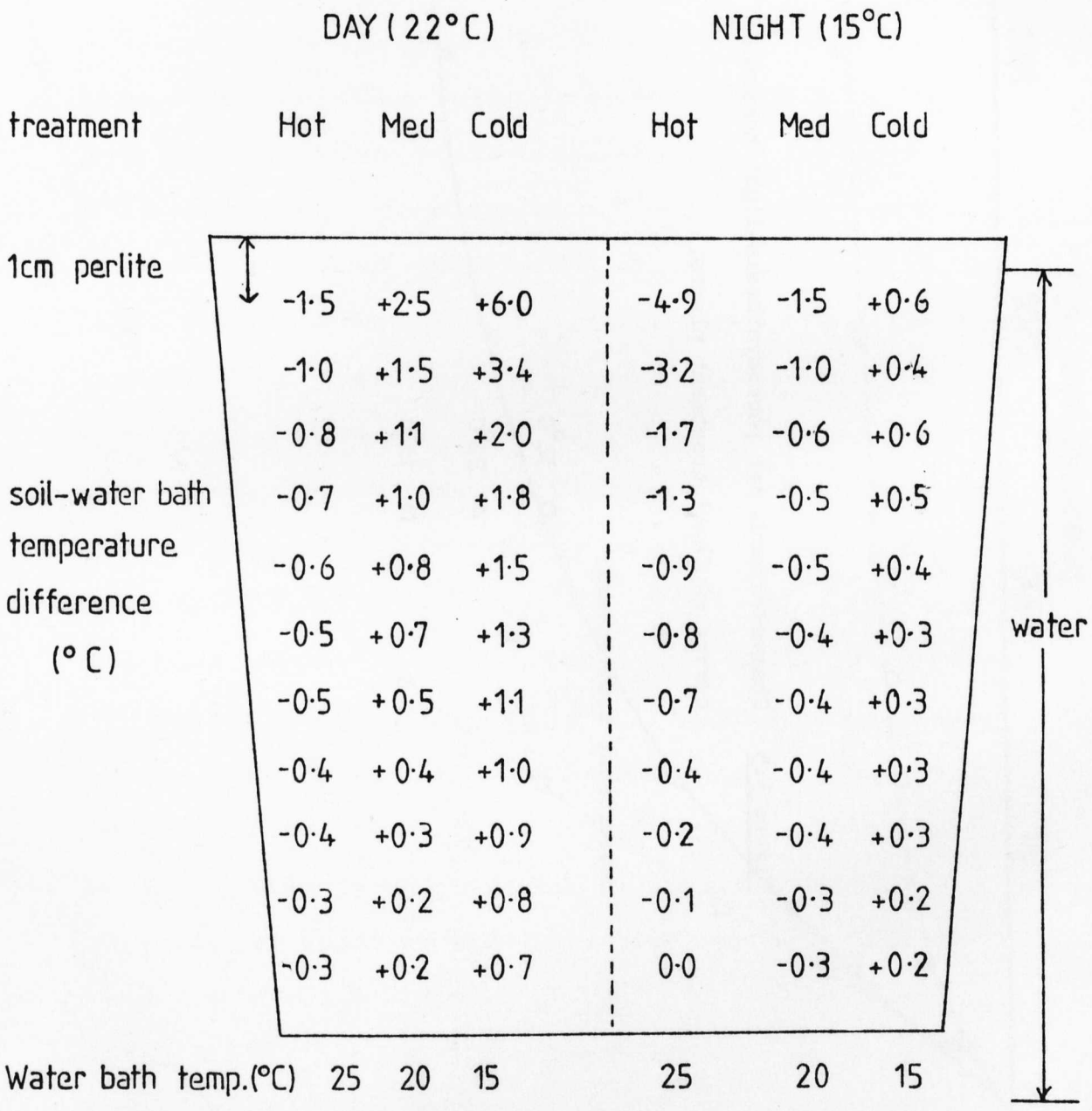


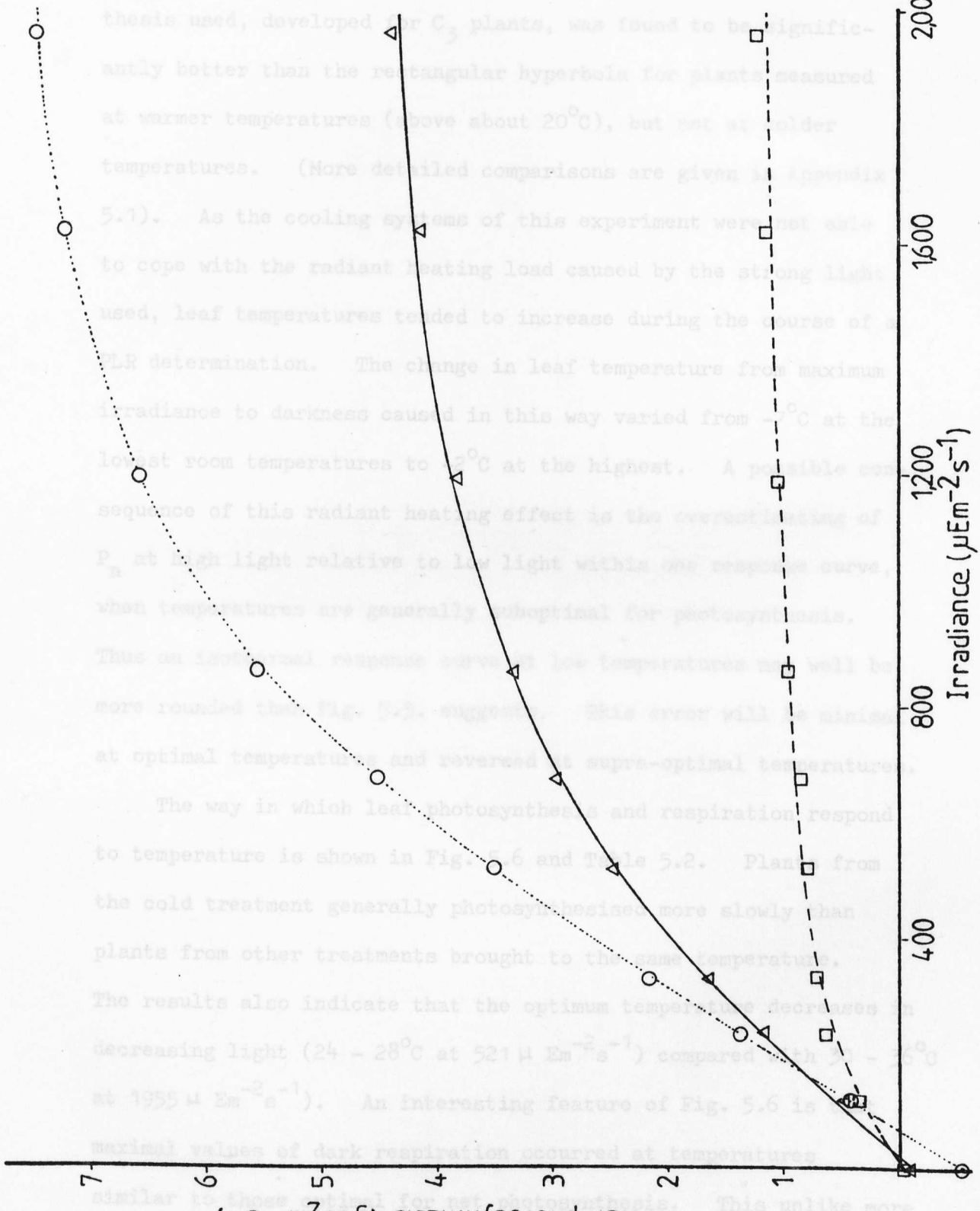
Figure 5.5 Characteristic net photosynthesis-light response curves of 'hot' treatment plants.

measurement temperature:

○ 32°C

△ 20°C

□ 11°C


Net photosynthesis ($gCO_2 m^{-2} s^{-1}$)
Irradiance ($\mu Em^{-2}s^{-1}$)
0
1
2
3
4
5
6
7
400
800
1200
1600
2000

temperatures. (Maximum irradiance in this experiment is approximately equivalent to full sunlight). The PLR model of photosynthesis used, developed for C_3 plants, was found to be significantly better than the rectangular hyperbola for plants measured at warmer temperatures (above about 20°C), but not at colder temperatures. (More detailed comparisons are given in Appendix 5.1). As the cooling systems of this experiment were not able to cope with the radiant heating load caused by the strong light used, leaf temperatures tended to increase during the course of a PLR determination. The change in leaf temperature from maximum irradiance to darkness caused in this way varied from -7°C at the lowest room temperatures to -2°C at the highest. A possible consequence of this radiant heating effect is the overestimating of P_n at high light relative to low light within one response curve, when temperatures are generally suboptimal for photosynthesis. Thus an isothermal response curve at low temperatures may well be more rounded than Fig. 5.5. suggests. This error will be minimal at optimal temperatures and reversed at supra-optimal temperatures.

The way in which leaf photosynthesis and respiration respond to temperature is shown in Fig. 5.6 and Table 5.2. Plants from the cold treatment generally photosynthesised more slowly than plants from other treatments brought to the same temperature. The results also indicate that the optimum temperature decreases in decreasing light (24 - 28°C at 521 μ $Em^{-2}s^{-1}$) compared with 30 - 36°C at 1955 μ $Em^{-2}s^{-1}$). An interesting feature of Fig. 5.6 is that maximal values of dark respiration occurred at temperatures similar to those optimal for net photosynthesis. This unlike more

Figure 5.6 Net photosynthesis response to temperature.

a) at irradiance 521 $\mu Em^{-2}s^{-1}$

● - 'hot' treatment

○ - 'cold' treatment

b) at irradiance 1955 $\mu Em^{-2}s^{-1}$

● - 'hot' treatment

○ - 'cold' treatment

at zero irradiance:

■ - 'hot' treatment

□ - 'cold' treatment

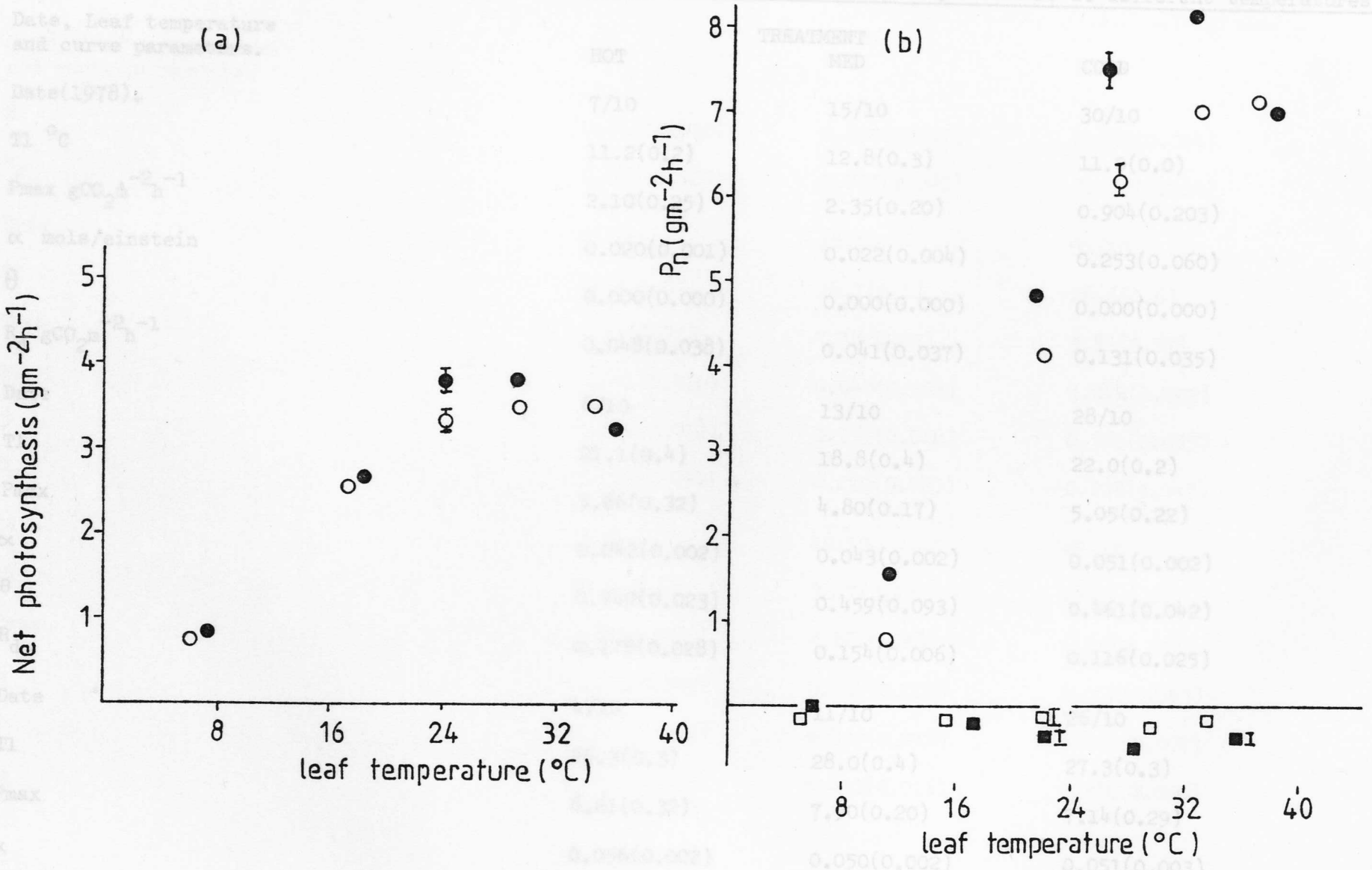

(a)
Net photosynthesis ($gm^{-2}h^{-1}$)
1
2
3
4
5
8
16
24
32
40
leaf temperature (°C)
(b)
P_n ($gm^{-2}h^{-1}$)
1
2
3
4
5
6
7
8
8
16
24
32
40
leaf temperature (°C)

Table 5.2. Net photosynthesis-light response curve parameters at different temperatures.

Date, Leaf temperature and curve parameters.	TREATMENT HOT	MED	COLD
Date(1978).	7/10	15/10	30/10
Tl ^{o}C	11.2(0.2)	12.8(0.3)	11.0(0.0)
Pmax $gCO_2m^{-2}h^{-1}$	2.10(0.25)	2.35(0.20)	0.904(0.203)
α mols/einstein	0.020(0.001)	0.022(0.004)	0.253(0.060)
θ	0.000(0.000)	0.000(0.000)	0.000(0.000)
R_d $gCO_2m^{-2}h^{-1}$	0.048(0.038)	0.041(0.037)	0.131(0.035)
Date	6/10	13/10	28/10
Tl	21.1(0.4)	18.8(0.4)	22.0(0.2)
Pmax	5.66(0.32)	4.80(0.17)	5.05(0.22)
α	0.042(0.002)	0.043(0.002)	0.051(0.002)
θ	0.749(0.023)	0.459(0.093)	0.461(0.042)
R_d	0.178(0.028)	0.154(0.006)	0.116(0.025)
Date	4/10	11/10	26/10
Tl	26.3(0.3)	28.0(0.4)	27.3(0.3)
Pmax	8.61(0.32)	7.90(0.20)	7.14(0.29)
α	0.056(0.002)	0.050(0.002)	0.051(0.003)

Table 5.2. (Contd)

Net photosynthesis-light response curve parameters at different temperatures.

Date, Leaf temperature and curve parameters.	Treatment HOT	MED	COLD
θ	0.851(0.020)	0.850(0.017)	0.766(0.024)
R_d	0.384(0.025)	0.277(0.020)	0.120(0.100)
Date	9/10	16/10	31/10
Tl	28.2(1.0)	28.7(0.1)	28.6(0.6)
Pmax	5.27(0.87)	7.18(0.02)	5.83(0.57)
α	0.041(0.010)	0.048(0.002)	0.042(0.002)
θ	0.711(0.072)	0.754(0.016)	0.761(0.055)
R_d	0.273(0.054)	0.270(0.025)	0.205(0.047)
Date	5/10	12/10	27/10
Tl	32.3(0.1)	32.7(0.1)	33.1(0.4)
Pmax	8.87(0.27)	8.86(0.16)	7.86(0.39)
α	0.055(0.002)	0.054(0.002)	0.052(0.003)
θ	0.915(0.007)	0.899(0.012)	0.867(0.007)
R_d	0.469(0.026)	0.402(0.018)	0.280(0.030)

Table 5.2. (contd)

Net photosynthesis-light response curve parameters at different temperatures

Date, Leaf temperature and curve parameters.	Treatment HOT	MED	COLD
Date	8/10	14/10	29/10
Tl	38.0(0.5)	38.6(0.1)	37.2(0.5)
Pmax	7.80(0.33)	7.09(0.31)	7.94(0.33)
α	0.047(0.002)	0.039(0.004)	0.048(0.007)
θ	0.903(0.04)	0.845(0.041)	0.894(0.007)
R_d	0.366(0.041)	0.361(0.020)	0.149(0.060)

usual descriptions which show dark respiration increasing with temperature until temperatures much higher than those optimal for photosynthesis (e.g. Doley and Yates, 1976). A likely reason for this response is that plants were generally in a low light environment, especially in the period immediately preceeding measurement. It is conceivable therefore that respiration was limited by substrate availability, and dark respiration consequently linked with levels of net photosynthesis attained during that PLR determination.

5.2.3.3. Resistance analysis.

To investigate the mechanism of plant photosynthetic response to temperature it is convenient to consider plant resistance to CO_2 movement, using the simple electrical analogue of three resistances in series; aerodynamic, r_a'; stomatal, r_s'; internal r_i'. (The superscript prime denoting resistance to CO_2 transfer, otherwise resistances refer to water vapour transfer). The resistance ra' is determined by chamber design and gas flow rate (0.48 scm^{-1} in this experiment). The resistance r_s can be calculated by a consideration of transpiration rate and ambient humidity, assuming the air is saturated in the substomatal cavity and water loss controlled by r_s and r_a. From r_s, the resistance r_s' can be calculated from the ratio of diffusion coefficients for H_2O and CO_2. The ratio r_s'/r_s was assumed to be 1.605 (Fuller et al, 1966) The resistance r_i' can be determined by subtracting r_s' and r_a' from the total resistance to CO_2 transfer to the ambient air, assuming zero concentration at the chloroplasts. According to this definition, r_i' includes both the physical

diffusion resistance between the sub-stomatal cavity and the reaction site, and the chemical resistance of the photosynthesis reaction.

Calculated values for r_s' and r_i' are given in Table 5.3. Negative values of r_i' at more favourable temperatures are physiologically anomalous, and a likely reason for these is the high vapour pressure in the equipment, caused by rapid transpiration rates, and responsible for condensation within the equipment. Calculated values of vapour pressure within the recirculating loop (containing the leaf chamber) reached 21 mbar, similar to saturated vapour pressures in the air surrounding the system. Even allowing for this error, photosynthesis at low temperatures appears to be limited by high internal resistance. This limitation is also reflected in the low values of θ at low temperatures, although the value $\theta = 0$ is also anomalous and may reflect distortion of the response by the radient heating error mentioned above. At more favourable temperatures r_i' is much reduced, and photosynthesis is more strongly correlated with r_s'. It is worth noting here that at low temperatures and with high internal resistances, the stomata were open, although substomatal CO_2 concentrations would be high. This suggests that the homeostatic mechanism suggested by Raschke (1975) and Cowan and Farquhar (1977) whereby stomata respond to substomatal CO_2 concentrations to optimise CO_2 assimilation with regard to water loss, may not be universal. It also suggests that at lower values of r_i', r_s' was limiting photosynthesis rather than responding to it.

Limiting values of quantum efficiencies at zero irradiance

Table 5.3. - Stomatal and internal resistance response to temperature.

Date, Leaf temperature	Treatment		
Stomatal and internal resistance	HOT	MED	COLD
Date	7/10	15/10	30/10
Tl ^{o}C	11.2	12.8	11.0
r_s' scm^{-1}	0.91(0.23)	0.52(0.14)	0.33(0.11)
r_i' scm^{-1}	12.2(1.0)	11.9(1.7)	22.8(1.9)
Date	6/10	13/10	28/10
Tl	21.1	18.8	22.0
r_s'	2.5(0.1)	1.2(0.1)	2.8(0.3)
r_i'	1.4(0.3)	3.7(0.1)	1.7(0.3)
Date	4/10	11/10	26/10
Tl	26.3	28.0	27.3
r_s'	1.9(0.1)	1.8(0.1)	2.2(0.2)
r_i'	0.32	0.58(0.12)	0.52(0.12)
Date	9/10	16/10	31/10
Tl	28.2	28.7	28.6
r_s'	2.5(0.3)	2.5(0.1)	4.9(1.5)

Table 5.3. (Contd)

Stomatal and internal resistance response to temperature.

Date, Leaf temperature	Treatment		
Stomatal and internal resistance	HOT	MED	COLD
r_i'	2.5(1.2)	0.37(0.02)	-0.33(0.62)
Date	5/10	12/10	27/10
Tl	32.3	32.7	33.1
r_s'	1.8(0.2)	1.5(0.1)	2.1(0.1)
r_i'	0.25(0.12)	-0.40(0.23)	0.08(0.27)
Date	8/10	14/10	29/10
Tl	38.0	38.6	37.2
r_s'	2.7(0.2)	3.6(0.0)	4.6(0.3)
r_i'	-0.44(0.13)	-0.75(0.43)	-0.33(0.62)

are not significantly different between treatments for the first two days of PLR determinations in each treatment (Table 5.3). The leaf temperatures on these two days were 26 - 28°C and 32 - 33°C respectively. Efficiencies of 0.050 - 0.056 mol CO_2/einstein of incident radiation agree well with the mean efficiencies for C_4 plants of 0.053 mol CO_2/absorbed einstein quoted by Ehleringer and Bjorkman (1977) (the absorption of photosynthetically active radiation by leaves exceeds 75% - Ehleringer and Bjorkman). Unlike the results of Ehleringer and Bjorkman however, quantum efficiencies in this experiment were not constant throughout the temperature range, but the errors already discussed may be responsible for this discrepancy. The efficiency of 0.253 mols CO_2/einstein calculated for the cold treatment plants at a measurement temperature of 11°C is physiologically impossible, and reflects the poor fit of the model to the measured response in this instance.

Measurements of photosynthesis after five days of various temperatures, show that rates did not attain the values achieved on the first day, at the same temperatures. There was also a much greater degree of variability among the plants of one treatment, indicating that some plants were irreversibly damaged by previous days measurements.

5.2.4. Discussion

It is difficult to compare photosynthetic characteristics from published measurements, because of the unknown effects of previous environmental conditions, as discussed above. Results

of Bird et al (1978), for maize grown in conditions similar to this experiment, show comparable photosynthetic rates. At 580 μ $Em^{-2}s^{-1}$ they obtained P_n values of 3 - 4 $gCO_2m^{-2}h^{-1}$ at an optimum temperature of about 23°C, compared with 3.5 - 4 $gCO_2m^{-2}h^{-1}$ at 521 μ $Em^{-2}s^{-1}$ and an optimum temperature of 26° - 30°C in this experiment. The higher temperature optimum may well be due to the tropical nature of the variety used in this experiment compared with the temperate variety of Bird et al. The results reported show that the irradiance level must be considered when discussing temperature optima for photosynthesis.

Fig. 5.6 indicates that plants grown in colder soils will have a poorer photosynthetic performance at typical field temperatures. At 27°C and 1000 μ $Em^{-2}s^{-1}$ the P_n values are approximately 5 and 6 $gm^{-2}h^{-1}$ in the cold and hot treatments respectively. If there was a corresponding 20% decrease in dry weight accumulation in the field, this would be roughly equivalent to 4 $gm^{-2}day^{-1}$ below the 20 $gm^{-2}day^{-1}$ typical of the better Kitale crops. From the correlation of crop growth against yield of Cooper (1979) the corresponding decrease of yield would be about 40 g/plant. The decrease in photosynthesis in this experiment was the result of a lowering of soil temperature (at approximate meristem depth) from about 23°C to 17°C (see Section 5.2.3.1) and these temperatures are close to the most extreme values likely to be encountered at the start and middle of the rainy season at Kitale.

The measurements therefore support the hypothesis that soil

temperature can affect growth and yield through its influence on photosynthesis rate. However, the size of the response is not consistent with the work of Cooper and Law (1978a), who found that a 1°C increase in soil temperature was associated with an increase of yield by 50 g/plant. Even larger yield differences appeared in 1977 where the difference in soil temperature was only 0.5°C (see Section 4).

6. DISCUSSION AND CONCLUSIONS

The work described in this thesis leads to a number of conclusions concerning soil temperature, the relations between maize growth and yield in the Kenya Highlands.

1) Plants grown in soils warmed by mulches initiate a greater number of leaves; but as early leaves on these plants are smaller, the increase in total leaf area produced is negligible. This observation indicates that the small differences in leaf area production observed in time of planting treatments are not a result of the associated changes in soil temperature. In addition, because standing dry weight increases linearly with time when the leaf area index exceeds about 3.5 small differences in leaf area cannot be responsible for the differences in growth rate (during the linear phase) observed in time of planting studies.

2) Soil temperature during early growth does not determine the number of spikelets initiated. Spikelet initiation occurs when the embryonic cob is above ground level, and consequently the initiation rate should be determined by air temperature rather than soil temperature. Mean air temperature varies little throughout the year at Kitale. Differences in grain yield that do occur as a result of changes in planting date, soil temperature (by use of mulches), and plant population are largely a result of differences in the number of initiated grains surviving to maturity. The direct cause of this development failure is still unknown.

3) Plants grown from seeds of different size had different weights 5 weeks after emergence but gave similar grain yields. Cooper (1978a) reported that mulched and unmulched plants reached

similar sizes at tasselling but gave different yields. These reports taken in conjunction, indicate that plant size per se at any stage is not a discriminant of yield. However plants from all experiments showed a relationship between crop growth rate during the linear phase and grain number.

4) Changes in soil temperature do not affect leaf photosynthetic efficiency enough to account for observed differences in crop growth rate of early and late planted maize.

Several other lines of evidence suggest that soil temperature alone may not be responsible for the time of planting effect at Kitale:

a) The decrease in soil temperature with the onset of the rainy season is not as marked as first suggested by Law and Cooper (1976), but is more typically about 2 - 3°C over the growing season. (c.f. Table 4.1) It is difficult to conceive a physiological process sensitive to such small soil temperature changes that could explain the yield differences associated with the time of planting effect at Kitale. Furthermore, it seems unlikely that the differences in growth rate observed in the 1977 experiment (a 30% decline - see Chapter 4) were the result of the associated 0.7°C decline in soil temperature during the early stages.

b) The equation of yield dependence on soil temperature quoted by Cooper and Law (1977) implies a base temperature for yield of 18.3°C; yet maize grown at higher altitudes with correspondingly lower soil temperatures yields more than maize grown at lower altitudes (Cooper, 1979). The equation also

shows a very large yield increase (about 25% of maximum yields) for 1°C increments in soil temperature over the range 19 - 23°C; yet polythene mulches which raise the temperature a further 5 - 6°C do not increase yields much above those of early planted maize. These observations cannot be reconciled unless there is a very sharply-defined critical temperature, typically experienced by early planted maize, below which yields are very temperature dependent and above which yields are unaffected.

c) As stated in Chapter 1, the time of planting effect is common to a very wide range of crops in a wide range of thermal environments, the common factor being the sequence of wet and dry seasons. This suggests that although soil temperature may play a part in seasonal variations in growth and yield of maize, there may be other causes common to these other crops and sites.

d) The association between soil temperature and yield is largely based on linear correlations from time of planting experiments. This correlation does not necessarily imply cause and effect. Allan (1972) found a similar correlation with accumulated rainfall, and both accumulated rainfall and decrease in soil temperature are largely associated with time elapsed from the start of the rainy season.

There is therefore a case for re-examining the hypothesis that decrease in soil temperature is the main cause of the time of planting effect exhibited by maize at Kitale, bearing in mind that polythene mulches raise the yields of late planted maize. Further work should assess the effects of soil heating by methods other than mulching. It is conceivable that different mechanisms

are responsible for the differences in yield observed in time of planting experiments and in mulching experiments. One possible mechanism is the availability of some nutrient, mineralised, released at the beginning of the rains and subsequently leached (as suggested by Birch, 1960) but made more available by warmer soils. Late planted maize does exhibit many of the potassium deficiency symptoms described by Peaslee and Moss, 1966, but no difference in the potassium content of the leaves of the 1977 experiment could be discerned (see Appendix 6.1). Thus there is a case for examining in greater depth the relationships between nutrient availability and uptake, root and shoot growth. Until soil and root changes are better understood, the time of planting effect will remain an enigma.

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A. 3.1. Dry matter and leaf area production - Mulch and seed size trial.

	Polythene mulch		Large seed		Medium seed		Small seed	
Days after planting	Shoot D.M.(g)	Leaf area(m^2)	Shoot D.M.(g)	Leaf area(m^2)	Shoot D.M.(g)	Leaf area(m^2)	Shoot D.M.(g)	Leaf area(m^2)
10	0.109		0.066		0.061		0.034	
	(0.004)		(0.003)		(0.003)		(0.002)	
17	0.616	0.016	0.409	0.010	0.302	0.008	0.164	0.005
24	3.13	0.063	1.84	0.037	1.34	0.028	0.784	0.017
28	6.38	0.101	3.23	0.058	2.63	0.049	1.98	0.037
38	23.4	0.275	12.5	0.165	9.51	0.141	7.07	0.106
53	74.4	0.656	50.0	0.480	48.7	0.456	36.7	0.381
	(1.7)	(0.015)	(2.1)	(0.015)	(2.1)	(0.016)	(2.3)	(0.017)
59	101	0.732	72.3	0.611	64.6	0.547	53.0	0.492
66	126	0.898	100	0.775	92.2	0.727	88.7	0.709
73	171	0.979	144	0.882	136	0.862	120	0.777
80	206	1.089	177	1.001	157	0.949	155	0.930
87	237	1.234	-	1.174	198	1.170	-	1.134
	(9.0)	(0.048)		(0.036)	(7.5)	(0.030)		(0.036)
94	274	1.143	240	1.144	257	1.216	259	1.238
101	330	1.309	277	1.333	275	1.120	272	1.237
115	366	1.334	351	1.498	307	1.268	321	1.284
130	494	1.454	456	-	408	1.341	394	-
141	493	-	-	-	396	-	-	-
	(20)	-	-	-	(13)			
152	534	-	-	-	529	-	-	-

A. 3.2.

Polythene mulch, seed size and final grain yield.

	Polythene mulch	Large seed	Medium seed	Small seed
Grain weight (g/plant)				
1st cob	171	152	148	153
2nd cob	9	7	11	15
Total	180(6)	159(8)	159(7)	168(7)
Grain number 1st cob	439	425	388	397
2nd cob	30	25	34	44
Total	467(17)	450(22)	423(22)	443(20)
1000 grain wt(g) 1st cob	392	362	395	393
2nd cob	300	274	376	361
Total	389(8)	361(10)	391(10)	390(8)
Total plant dry weight(g)	531(13)	463(15)	487(14)	496(13)
Harvest index (%)	34	34	33	33.9
Number cobs/plant	1.17	1.12	1.17	1.28
Estimated yield loss due to bird damage (%)	2.5	1.1	1.6	2.3

A. 3.3. (a) Population trial sample data.

Population	Leaf appearance		Leaf area(m^2)		Total dry Wt.(g)	
	Low	High	Low	High	Low	High
Days after planting						
27	8.4	8.4				
34	10.5	10.3	0.106	0.102	7.67	6.47
			(0.005)	(0.005)	(0.48)	(0.39)
41	12.6	12.4				
47	14.6	13.9	0.353	0.312	34.1	24.2
55	16.6	15.3	0.566	0.405	64.1	40.7
62	18.4	16.6	0.680	0.542	99.6	59.7
69	19.8	17.7	0.833	0.617	138	74.3
			(0.028)	(0.013)	(5.2)	(2.9)
75	20.6	18.5	0.957	0.669	192	78.6
83	22.1	20.0	076	0.764	268	99.9
90	22.5	20.9	1.195	0.819	300	118
97					328	167
111			1.188	0.992	453	202
			(0.027)	(0.035)	(158)	(10.5)

A. 3.3. (b)

Population trial - Spikelet numbers.

	Low Population			High Population		
	1st cob	2nd cob	3rd cob	1st cob	2nd cob	3rd cob
Spikelet number per row						
62 d.a.p.	18.0	14.5	12.0	17.3	13.0	8.8
	(1.9)	(1.6)	(1.1)	(1.6)	(1.5)	(1.2)
69	34.7	31.5	26.6	30.8	25.2	21.3
	(1.5)	(2.6)	(1.7)	(2.1)	(2.3)	(2.9)
75	40.2	38.7	36.0	36.2	33.0	28.4
	(2.4)	(2.8)	(2.4)	(2.0)	(1.2)	(2.5)
83	53.3	50.2	45.2	42.2	42.0	34.5
	(2.0)	(2.1)	(1.5)	(1.0)	(2.1)	(1.8)
90	57.7	53.2	57.0	54.0	48.5	44.3
	(1.6)	(2.2)	(2.6)	(1.9)	(2.2)	(1.8)
Spikelet row number	12.7	13.0	12.9	13.2	13.0	12.8
	(0.4)	(0.4)	(0.3)	(0.3)	(0.3)	(0.4)

A.- 3.4.

Population density and grain yield.

	Population plants/ha	Low 17,800	Medium* 44,000	High 111,000
Grain number/plant				
	1st cob	592 (20)	448	245 (45)
	2nd cob	178 (43)	19	0
	Total	770 (52)	467 (7.4)	245 (45)
1,000 grain wt	1st cob	403 (11)	356	304 (23)
	2nd cob	350 (24)	292	0
	Total	393 (11)	353 (11)	304 (23)
Grain yield. g/plant	1st cob	238 (9.9)	160	65.8 (12.8)
	2nd cob	61.2 (15.4)	5.4	0
	Total	300 (19.3)	164 (2.9)	65.8 (12.8)
Grain yield.g/m^2		534	721	730
cobs/plant		1.6	1.06	0.7

* From an adjacent trial, planted on the same day. (Cooper and Law, 1978b)
Note all grain Wts quoted at zero moisture.

A. 4.1 Leaf appearance of mulched plants.

a) M1

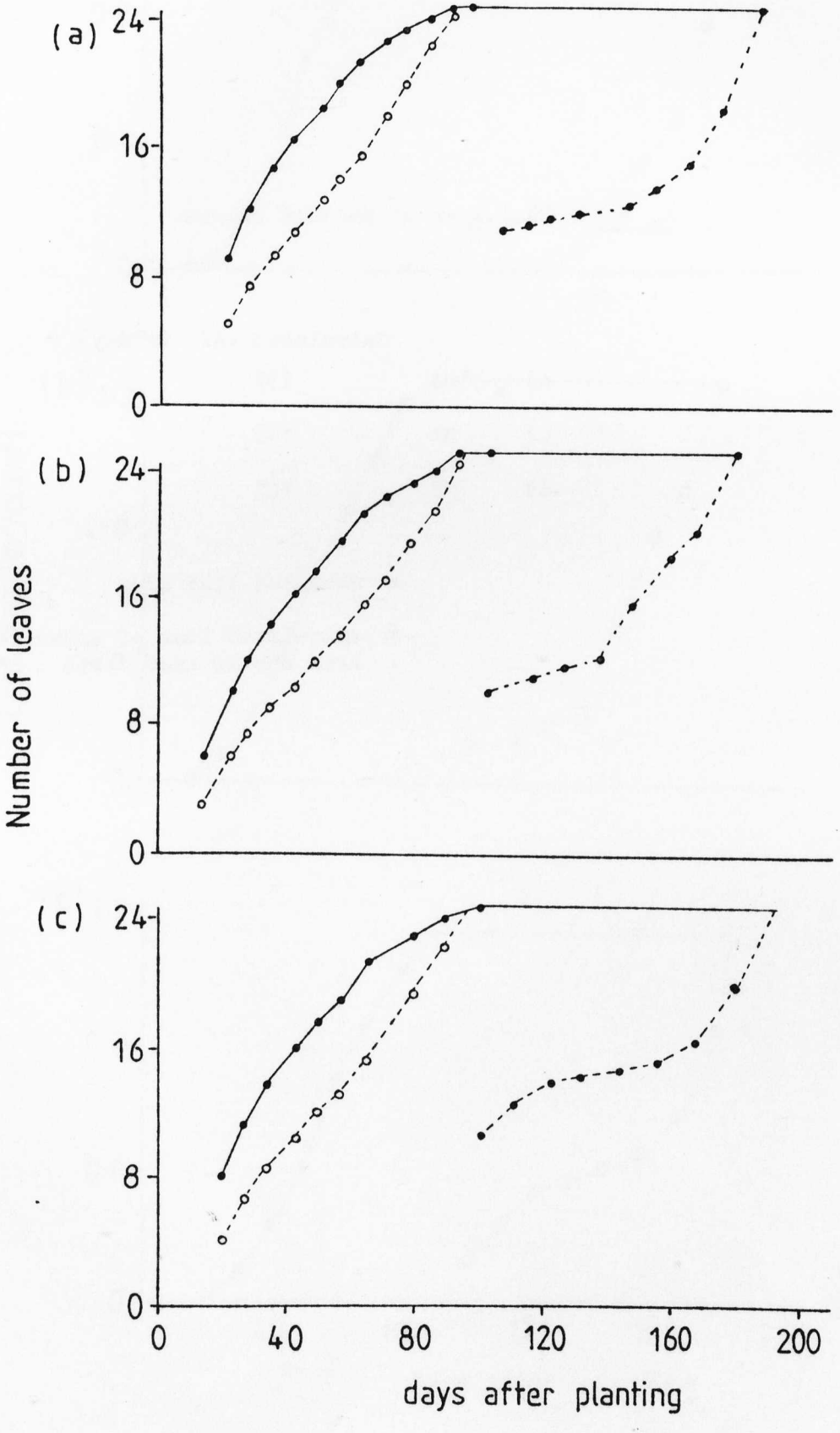
b) M2

c) M3

●—● appearance of leaf tip

o--o appearance of leaf collar

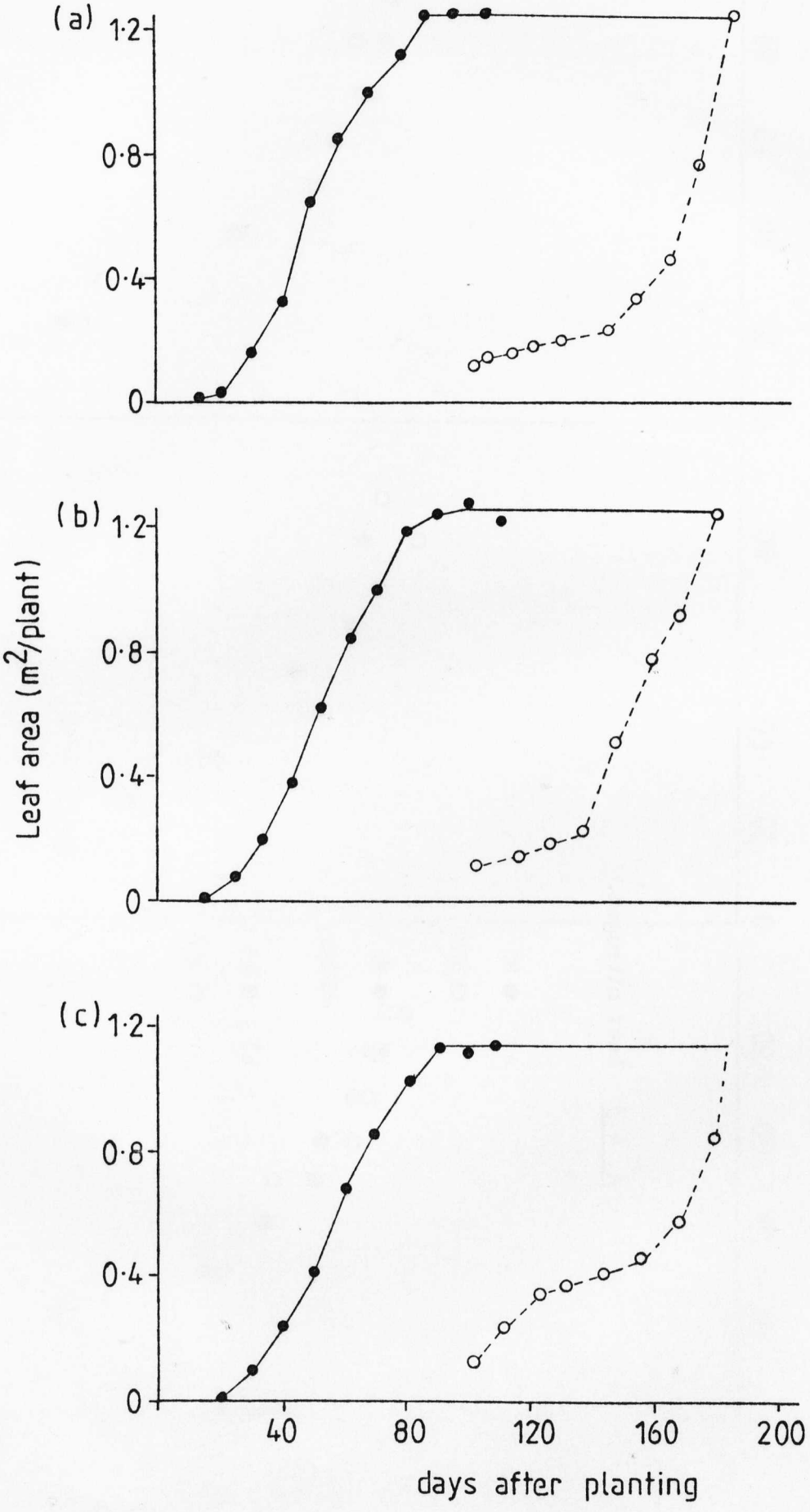
●--● death of leaf


(a)
(b)
(c)
24
16
8
0
Number of leaves
0
40
80
120
160
200
days after planting

A. 4.2 Leaf area of mulched plants.

		Calculated LAD (m^2day)
a)	M1	137
b)	M2	119
c)	M3	105

- ● measured leaf area
- o calculated loss of green leaf area due to leaf death


(a)
1·2
0·8
0·4
0
(b)
1·2
0·8
0·4
0
Leaf area (m²/plant)
(c)
1·2
0·8
0·4
0
40
80
120
160
200
days after planting

A. 4.3 Leaf nitrogen.

a) ● M1

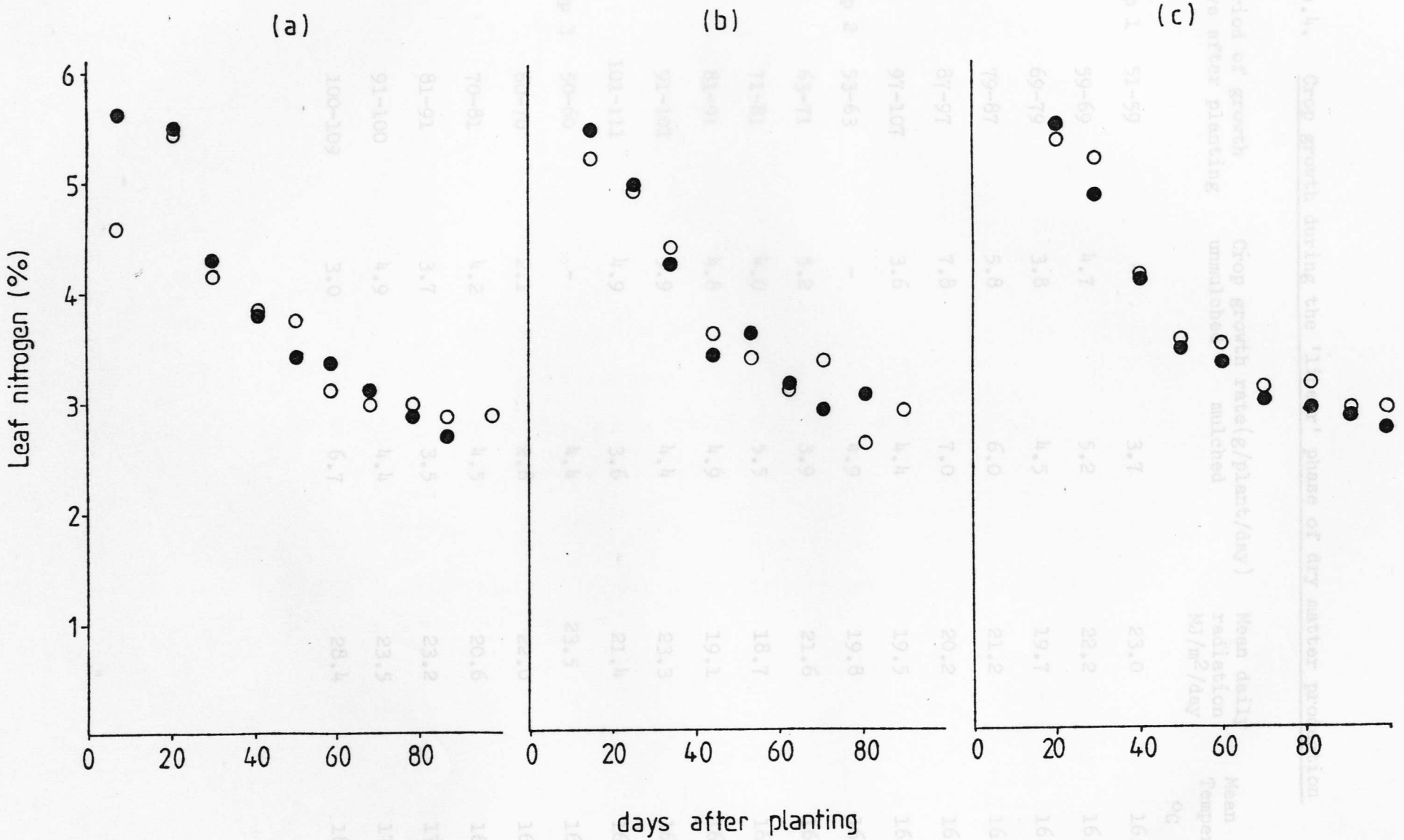
○ UM1

b) ● M2

○ UM2

c) ● M3

○ UM3


(a)
(b)
(c)
Leaf nitrogen (%)
6
5
4
3
2
1
0
20
40
60
80
days after planting

A 4.4. Crop growth during the 'linear' phase of dry matter production

Period of growth Days after planting		Crop growth rate(g/plant/day) unmulched	mulched	Mean daily radiation $MJ/m^2/day$	Mean Temperature °C
Top 1	51-59	-	3.7	23.0	16.9
	59-69	4.7	5.2	22.2	16.7
	69-79	3.8	4.5	19.7	16.2
	79-87	5.8	6.0	21.2	16.6
	87-97	7.8	7.0	20.2	16.2
	97-107	3.6	4.4	19.5	16.2
Top 2	53-63	-	4.9	19.8	16.1
	63-71	5.2	3.9	21.6	16.8
	71-81	4.0	5.5	18.7	16.1
	81-91	4.8	4.9	19.1	16.1
	91-101	5.9	4.4	23.3	16.0
	101-111	4.9	3.6	21.4	16.6
Top 3	50-60	-	4.4	23.5	16.2
	60-70	2.1	2.8	22.0	16.1
	70-81	4.2	4.5	20.6	16.3
	81-91	3.7	3.5	23.2	17.1
	91-100	4.9	4.4	23.5	17.2
	100-109	3.0	6.7	28.4	18.0

A. 4.5 Weight changes of plant parts after flowering.

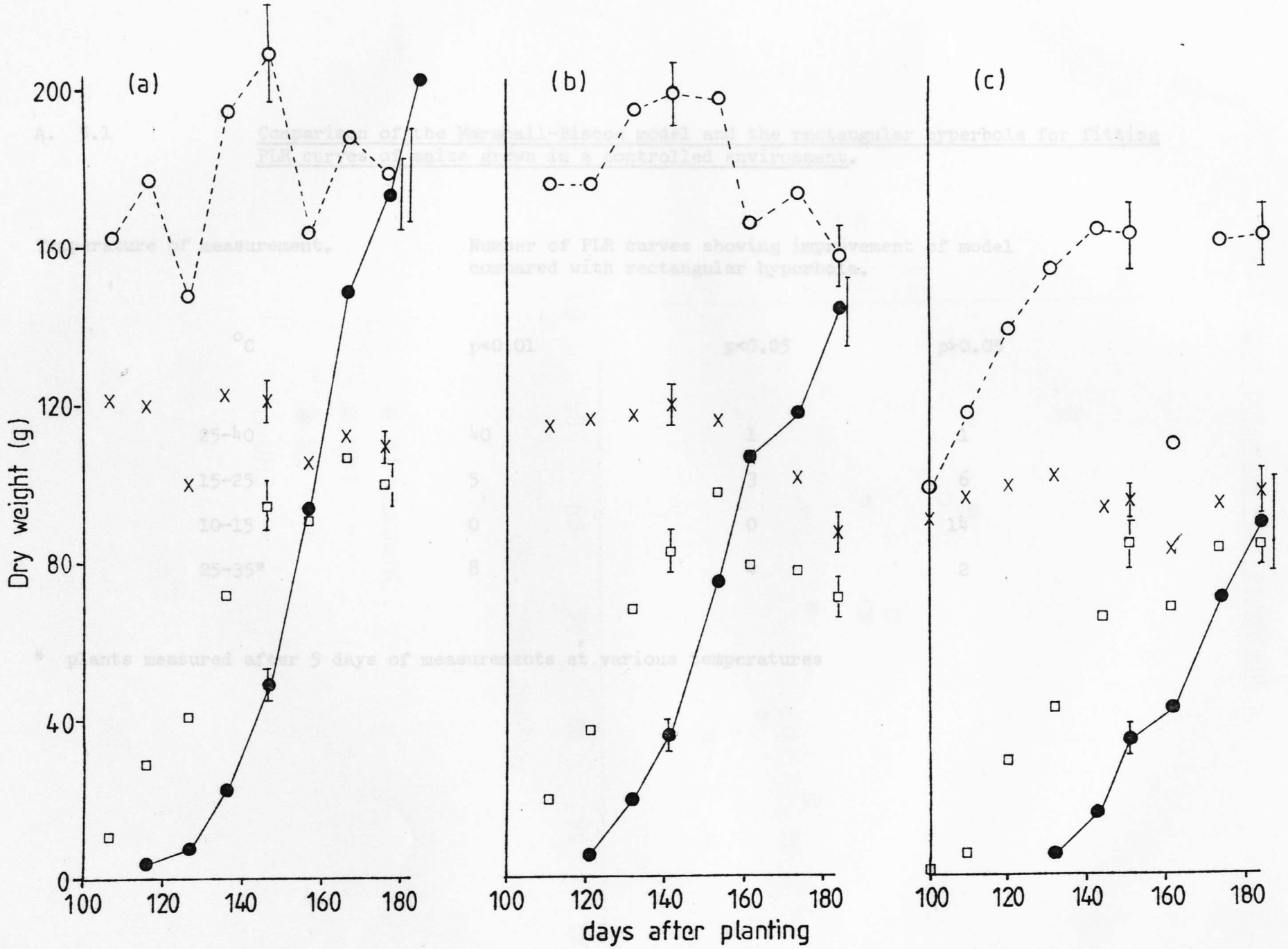
a) UM1 b) UM2 c) UM3

○ stem dry weight

X leaf (blade and sheath) dry weight

□ husk and core dry weight

● grain dry weight

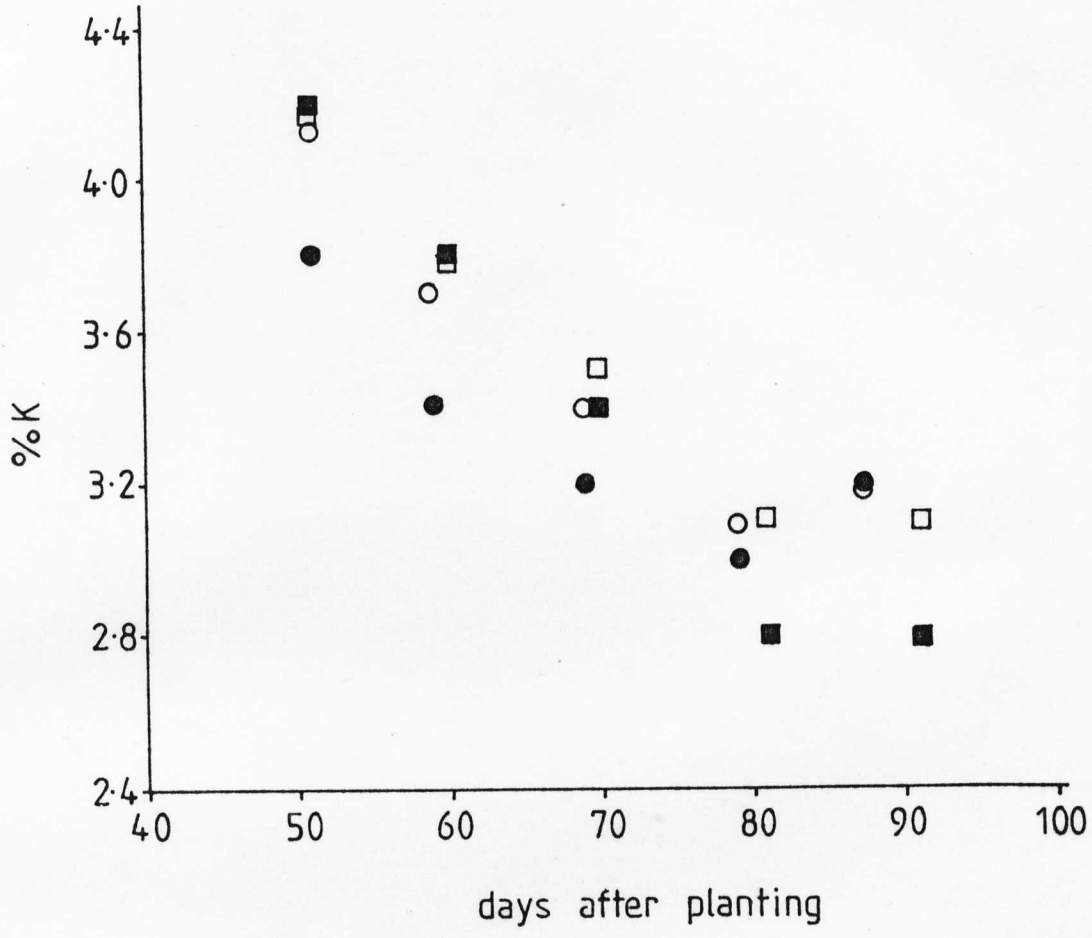

(a)
(b)
(c)
Dry weight (g)
days after planting
0
40
80
120
160
200
100
120
140
160
180

A. 5.1 Comparison of the Marshall-Biscoe model and the rectangular hyperbola for fitting PLR curves of maize grown in a controlled environment.

Temperature of measurement.	Number of PLR curves showing improvement of model compared with rectangular hyperbola.		
°C	p<0.01	p<0.05	p>0.05
25-40	40	1	1
15-25	5	3	6
10-15	0	0	14
25-35*	8	4	2

* plants measured after 5 days of measurements at various temperatures

A 6.1 Leaf potassium -1977 experiment.



● M1 treatment
○ UM1 "
■ M3 "
□ UM3 "

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....DEPT OF PHYSIOLOGY AND ENVIRONMENTAL STUDIES.

TITLE OF THESIS.....MAIZE GROWTH AND TEMPERATURE....
..IN THE KENYA HIGHLANDS.....

.....

DEGREE FOR WHICH SUBMITTED.....Ph.D.....

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